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BIOLOGY OF THE VERTEBRATES



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BIOLOGY OF THE VERTEBRATES

A COMPARATIVE STUDY
OF MAN AND HIS ANIMAL ALLIES

27767 BY

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Preface

"A textbook is an attempt to establish a happy relationship between teacher and pupil. Of the trinity of text, teacher, and pupil, the pupil is without doubt the most important, but even after the teacher is labeled 'emeritus,' and direct classroom contact with the pupil is a thing of the past, there still remains a possible mission for the old textbook to accomplish.

"Hence this Indian summer revision, after many years of trying to tell the fascinating story of vertebrate life to more or less attentive students. It has been fun "

These words, jotted down for possible use in the preface to a third edition of this book, were the last to come from the hand of Professor Walter. The *fun* which he had in teaching his classes and in preparing the first two editions of this text, the humor which he wove into this fabric, have made the study of Comparative Anatomy more interesting to thousands of us.

For the opportunity to assume the responsibility for the future of the *Biology of the Vertebrates*, I am indebted to Mrs. Walter, who has done everything within her power to make the preparation of this third edition the enjoyable undertaking which it has been.

In the present edition major portions of the chapters on vertebrate types, embryology, skeleton, nervous system, and sense organs have been rewritten, while less extensive changes have been made in other sections. I hope that in so doing I have still retained something of the flavor of previous editions.

Through the generous cooperation of The Macmillan Company, publishers, it has been possible to use new copy for over four hundred illustrations, some of which are redrawings of figures previously used, but many of which are new to the text. About half of this new illustrative material was prepared by Dr. Margaret Esther Potzger. Of the remainder many were drawn by Dr. C. J. Hylander. A number of illustrations were borrowed from a variety of sources. In this connection I wish to express my appreciation to The Blakiston Company, Henry Holt and Company, Houghton Mifflin Company, W. B. Saunders Company, and The Williams and Wilkins Company, as well as The Macmillan Company, for their permissions to use

illustrations from books for which they hold the copyrights, as duly noted wherever such illustrations appear in the text.

In the preparation of this edition I have been greatly aided by the advice and assistance given me by many who have used the earlier editions in their courses, or who, for other reasons, have read them critically. While it is not possible to enumerate all who have been helpful, I should like to make special mention of several of my colleagues in the Department of Biology at The City College to whom I am especially indebted, namely: Professors H. Herbert Johnson, Percy L. Bailey, Jr., Raymond W. Root, James I. Kendall, Herman T. Spieth, and Donald W. Farquhar. But my greatest indebtedness is to the librarians at the American Museum of Natural History who expedited my work by their cheerful and efficient help in my search for references, regardless of the difficulties involved.

L.P.S.

Floral Park, N. Y.

Table of Contents

PART ONE: THE BACKGROUND

CHAPTER I. Chordate Characters	3
I. Type Study, 3	
II. Comparative Study, 4	
III. Essential Features of Every Animal Type, 5	
IV. Symmetry, 6	
V. Metamerism, 9	
VI. Coelom, 9	
VII. Chordate Characteristics, 9	
1. Notochord, 9	
2. Dorsal Hollow Central Nervous System, 10	
3. Pharyngeal Breathing Device, 10	
4. Ventral Heart, 11	
5. Closed Blood System, 11	
6. Hepatic Portal System, 11	
7. A Post-Anal Tail, 11	
8. Red Blood Cells, 12	
VIII. Comparative Diagrams of Chordates and Non-Chordates, 12	
CHAPTER II. Kinds of Vertebrates (Classification)	13
I. Taxonomy, 13	
II. Scientific Names, 15	
III. A Roll Call of Chordata, 17	
A. Borderline Chordates, 17	
1. Subphylum Hemichordata, 17	
2. Subphylum Urochordata, 18	
3. Subphylum Cephalochordata, 21	
B. Subphylum Vertebrata (Craniata), 25	
1. Class Cyclostomata, 25	
2. Class Pisces, 27	
a. Subclass Chondrichthyes, 29	
(1) Order Gladoselachii, 29	
(2) Order Elasmobranchii, 30	
(3) Order Holocephali, 31	
b. Subclass Osteichthyes, 32	
(1) Order Crossopterygii, 32	
(2) Order Dipnoi, 33	
(3) Order Actinopterygii, 33	
(a) Suborder Chondrostei, 34	

- (b) Suborder Holostei, 35
 - (c) Suborder Teleostei, 35
- 3. Class Amphibia, 35
 - (1) Order Stegocephalia, 39
 - (2) Order Gymnophiona, 40
 - (3) Order Urodela (Caudata), 40
 - (4) Order Anura (Salientia), 42
- 4. Class Reptilia, 43
 - (1) Extinct Reptiles, 45
 - (2) Order Rhynchocephalia, 48
 - (3) Order Chelonia, 48
 - (4) Order Squamata, 49
 - (5) Order Crocodilia, 52
- 5. Class Aves, 52
 - a. Subclass Archacornithes, 54
 - b. Subclass Neornithes, 55
- 6. Class Mammalia, 57
 - a. Subclass Prototheria, 58
 - Order Monotremata, 58
 - b. Subclass Metatheria, 59
 - Order Marsupialia, 59
 - c. Subclass Eutheria, 60
 - (1) Order Insectivora, 62
 - (2) Order Dermoptera, 63
 - (3) Order Chiroptera, 63
 - (4) Order Carnivora, 65
 - (5) Order Rodentia, 65
 - (6) Order Primates, 67
 - (7) Order Edentata, 70
 - (8) Order Pholidota, 71
 - (9) Order Tubulidentata, 72
 - (10) Order Perissodactyla, 72
 - (11) Order Artiodactyla, 73
 - (12) Order Proboscidea, 75
 - (13) Order Hyracoidea, 77
 - (14) Order Sirenia, 77
 - (15) Order Cetacea, 78

CHAPTER III. The Distribution of Animals in Space (Chorology and Ecology)

- I. The Point of View, 81
- II. Ecology and Chorology, 82
- III. Habitats, 82
- IV. The Laws of Distribution, 83
- V. Malthus' Law of Overpopulation, 84
- VI. Factors Inducing Expansion, 85
 - 1. The Food Problem, 85
 - 2. Change of Habitat, 85
- VII. Means of Dispersal, 86
- VIII. Factors of Repression, 89
 - 1. Inadequate Means of Dispersal, 89
 - 2. Non-Adaptability to New Conditions, 89

3. Barriers, 90

IX. Classification of Life Realms, 91

CHAPTER IV. The Distribution of Animals in Time (Palaeontology) 95

- I. Vanishing Species, 95
- II. Fossils, 96
 - 1. Former Ideas about Fossils, 97
 - 2. Conditions of Fossilization, 97
 - 3. Uses of Fossils, 99
 - 4. Kinds of Fossils, 100
- III. Imperfections in the Record, 101
- IV. A Geologic Time Scale, 102
- V. Pictet's Palaeontological Laws, 104

CHAPTER V. Man in the Making (Anthropology) 106

- I. The Ancient History of Man, 106
- II. Tradition and Evidence, 107
- III. The Habitable Earth, 108
- IV. The Time Required, 108
- V. Archaeological Chronometers, 110
 - 1. Kitchen Middens, 110
 - 2. Pile Dwellings, 110
 - 3. Painted Grottoes, 111
 - 4. Large Stone Monuments, 113
 - 5. Tools and Weapons, 114
- VI. Human Fossils, 120
 - 1. Java "Ape-man" (*Pithecanthropus*), 120
 - 2. Peking Man (*Sinanthropus*), 122
 - 3. Heidelberg Man, 122
 - 4. Piltdown Man, 123
 - 5. Neanderthal Man, 124
 - 6. Cro-Magnon Man, 126
- VII. Time Scales, 127
- VIII. Conclusions, 128

CHAPTER VI. Units of Structure (Cytology) 129

- I. The Cell Theory, 129
- II. A Typical Cell, 129
- III. Cytomorphosis, 130
- IV. Cell Differentiation, 131
- V. Chromosomes, 133
- VI. Mitosis, 133
- VII. Fertilization, 136
- VIII. The Determination of Sex, 138
- IX. A World of Billions, 140

CHAPTER VII. Division of Labor in Tissues (Histology) 141

- I. Tissues, 141
- II. Fluid Tissues, 142
- III. Epithelial Tissues, 142
- IV. Connective and Supporting Tissues, 143

- 1. Connective Tissues, 143
- 2. Supporting Tissues, 145
 - (a) Cartilage, 145
 - (b) Bone, 147
- V. Muscle Tissue, 152
 - 1. Smooth Muscle, 153
 - 2. Striated Muscle, 153
 - 3. Cardiac Muscle, 154
- VI. Nerve Tissue, 154

CHAPTER VIII. The Development of the Individual (Embryology)

156

- I. The Starting Point, 156
- II. The Necessary Partners, 157
 - 1. Differentiation of the Germ Cells, 157
 - 2. Kinds of Sperm, 157
 - 3. Kinds of Eggs, 158
- III. Development of a Chordate, 159
 - 1. Cleavage, 160
 - 2. The Blastula, 160
 - 3. The Gastrula, 160
 - 4. Formation of the Nervous System, 162
 - 5. Formation of Notochord and Mesoderm, 164
 - 6. Differentiation of the Mesoderm, 164
 - 7. Emigration of the Mesenchyme, 165
 - 8. Assembling of the Digestive Tube, 166
 - 9. The Fate of the Germ Layers, 167
- IV. Early Development of Telolecithal Eggs, 168
- V. Early Development of Mammals, 173
- VI. The Major Cavities, 176
- VII. Organization Centers, 178
- VIII. Soma and the Germ Line, 180
- IX. The Succession of Generations, 181

CHAPTER IX. Biological Discords (Pathology)

182

- I. The Point of View, 182
- II. Deviations from the Normal, 183
- III. Disease, 183
- IV. Disturbances That Work Ill, 184
 - 1. Internal Disturbances, 184
 - (a) Formative Disturbances, 184
 - (b) Mechanical Interferences, 185
 - (c) Responsive Maladjustments, 185
 - (d) Hereditary Handicaps, 185
 - 2. External Disturbances, 186
 - (a) Thermal Factors, 186
 - (b) Chemical Factors, 187
 - (c) Barometric Factors, 187
 - (d) Mechanical Factors, 187
 - (e) Biological Factors, 187
- V. Sources of Pathological Knowledge, 188
- VI. The Control of Disease, 191

PART TWO: THE MECHANISM OF METABOLISM AND REPRODUCTION

CHAPTER X. A Jack of All Trades (The Integument) 195

- I. In General, 195
- II. Uses of the Integument, 196
 1. Protection, 196
 2. Reserve Storage of Food, 197
 3. Regulation of Heat, 198
 4. Sensation, 199
 5. Excretion, 200
 6. Secretion, 200
 7. Respiration, 200
 8. Locomotion, 201
- III. The Human Skin, 201
 1. Macroscopic, 201
 2. Microscopic, 203
 3. Embryonic, 206
- IV. Comparative Anatomy of the Integument, 207
 1. Invertebrate Integuments, 207
 2. Tunicates, 208
 3. Amphioxus, 208
 4. Cyclostomes, 209
 5. Amphibians, 210
 6. Scaly Forms, 211
 7. Birds, 213
 8. Mammals, 213
- V. Derivatives of the Integument, 214
 1. Glands, 214
 - (a) In General, 214
 - (b) Invertebrate Skin Glands, 215
 - (c) Vertebrate Glands, 216
 - (d) Sweat Glands, 219
 - (e) Sebaceous Glands, 220
 - (f) Other Alveolar Integumentary Glands, 221
 - (g) Mammary Organs, 222
 2. Scales, 229
 - (a) Fishes, 229
 - (b) Amphibians, 232
 - (c) Reptiles, 232
 - (d) Birds, 233
 - (e) Mammals, 233
 3. Horns, 233
 - (a) Keratin-Fiber Horns, 234
 - (b) Antlers, 234
 - (c) Pronghorns, 236
 - (d) Hollow Horns, 236
 4. Digital Tips, 237
 - (a) Claws, 237
 - (b) Hoofs, 239
 - (c) Nails, 240
 5. Miscellaneous Corneal Structures, 241
 6. Feathers, 243

- 7. Hair, 249
- 8. Friction Ridges, 257

CHAPTER XI. Intake Apparatus (Digestive System) 261

- I. In General, 261
 - 1. The Whirlpool of Life, 261
 - 2. Rate of Living, 261
 - 3. Hunger and Thirst, 262
 - 4. The Intake Mechanism of Animals and Plants Contrasted, 262
 - 5. The Mission of the Food Tube, 264
 - 6. Kinds of Feeders, 264
- II. The Food Tube, 265
 - 1. Its Evolution, 265
 - 2. Increase in Digestive Surface, 266
 - (a) Increase in Diameter, 266
 - (b) Increase in Length, 267
 - (c) Internal Folds, 268
 - (d) Supplementary Diverticula, 268
 - 3. Development, 270
 - 4. Histology, 270
 - 5. Regions of the Tube, 271
- III. Ingressive Zone, 272
 - 1. Food Capture and Prehension, 272
 - 2. The Mouth Aperture and Lips, 274
 - 3. Buccal Cavity, 275
 - 4. Oral Cavity, 277
 - 5. Tongue, 280
 - 6. Teeth, 287
 - (a) Structure, 287
 - (b) Development, 287
 - (c) Number, 290
 - (d) Succession, 291
 - (e) Situation, 292
 - (f) Attachment, 293
 - (g) Movement, 294
 - (h) Differentiation, 294
 - (i) Dental Formulæ, 296
 - (j) Origin of the Molars, 298
 - (k) Unusual Teeth, 299
 - (l) The Trend of Human Teeth, 300
- IV. Progressive Zone, 301
 - 1. Pharynx, 301
 - 2. Esophagus, 304
 - 3. Stomach, 306
- V. Degressive Zone, 311
 - 1. The Small Intestine, 311
 - 2. Glands, 314
 - (a) Liver, 315
 - (b) Pancreas, 319
 - (c) Intestinal Glands, 322
- VI. Egressive Zone, 324
- VII. The Essentials of Digestion, 326

VIII. Mesenteries, 326

CHAPTER XII. Internal Transportation (Circulatory System) 329

- I. In General, 329
- II. Blood and Lymph (The Carriers), 330
 1. Uses of the Blood, 330
 - (a) Equilibration of Water Content, 330
 - (b) Liberation of Energy, 331
 - (c) Distribution of Food, 331
 - (d) Regulation of Temperature, 331
 - (e) Transmission of Chemical Substances, 331
 - (f) Defence against Parasitic Invasion, 331
 - (g) Disposal of Cell Wreckage, 331
 - (h) Chemical Elaboration, 332
 - (i) Clinical Diagnosis, 332
 2. Amount of Blood, 332
 3. Erythrocytes, 332
 4. Leucocytes, 335
 5. Thrombocytes, 338
 6. Plasma, 339
- III. Blood Channels In General, 340
 1. The Evolution of Organic Irrigation, 340
 2. General Plans of Circulation, 341
 - (a) Annelid Plan, 341
 - (b) Amphioxus Plan, 342
 - (c) Gill Plan of Fishes, 342
 - (d) Lung Plan of Mammals, 343
 3. Structure of Blood Vessels, 344
 4. The Role of Capillaries, 346
- IV. Origin of Circulatory Systems, 348
- V. The Heart, 351
 1. In General, 351
 2. Embryonic Development, 352
 3. Evolution, 353
 - (a) Single-Circuit Hearts, 354
 - (b) Transitional Hearts, 356
 - (c) Double Hearts, 359
 4. Size and Position, 359
 5. Valves, 360
 6. The Work of the Heart, 361
- VI. Arteries and Their Transformations, 364
- VII. Venous Routes, 368
 1. In General, 368
 2. Development of Veins in Elasmobranchs, 370
 3. Evolution, 372
- VIII. Lymphatics, 377

CHAPTER XIII. The Release of Energy (Respiratory System) 382

- I. In General, 382
 1. The Respiratory Environment, 382
 2. The Exchange of Gases, 383
 3. The Essentials for Any Respiratory Device, 384

	4. Different Kinds of Respiratory Mechanisms, 385	
II.	Gills, 387	
	1. Invertebrate Gills, 389	
	2. Primitive Gills of Amphioxus and Tunicates, 389	
	3. Cyclostome Gills, 390	
	4. Elasmobranch and Holocephalan Gills, 391	
	5. Ganoid and Teleost Gills, 393	
	6. Dipnoan Gills, 395	
	7. Amphibian Gills, 395	
	8. Gill Structures in Land Vertebrates, 397	
III.	Swim Bladder, 397	
IV.	Lungs, 401	
	1. General Plan, 401	
	2. Air Passages, 403	
	(a) Nasal Chamber and Pharynx, 403	
	(b) Trachea, 403	
	(c) Bronchi, 405	
	(d) Bronchioles, 405	
	(e) Alveoli, 405	
	3. Phylogeny, 406	
	(a) Dipnoans, 406	
	(b) Amphibians, 406	
	(c) Reptiles, 408	
	(d) Birds, 408	
	(e) Mammals, 412	
	4. Pleural Envelopes, 413	
	5. Origin of the Lungs, 413	
V.	Devices for Securing Air, 414	
	1. Fishes, 415	
	2. Amphibians, 416	
	3. Reptiles, 417	
	4. Birds, 417	
	5. Mammals, 418	
VI.	Voice Apparatus, 420	
	1. Amphibians, 421	
	2. Reptiles and Birds, 422	
	3. Mammals, 423	
CHAPTER XIV.	Outgo Apparatus (Excretory System)	427
I.	Excretion, 427	
II.	Kidneys, 429	
	1. Form, 429	
	2. Position, 430	
	3. Gross Structure of the Mammalian Kidney, 431	
	4. A Urinary Unit, 432	
	5. Urine, 435	
III.	Urinary Ducts, 436	
IV.	Bladders, 437	
V.	The Succession of Kidneys, 440	
	1. In General, 440	
	2. The Nephridial Apparatus of Amphioxus, 440	
	3. Pronephros, 441	

4. Mesonephros, 443
5. Metanephros, 445

CHAPTER XV. The Preservation of Species (Reproductive System) 447

- I. The Significance of Reproduction, 447
- II. Methods of Reproduction, 448
- III. The Essential Reproductive Cells, 449
 1. Sperm Cells, 449
 2. Eggs, 451
- IV. Secondary Reproductive Apparatus, 454
 1. Gonads, 454
 - (a) Testes, 456
 - (b) Ovaries, 460
 - (c) Hermaphroditism, 463
 - (d) Gametogenesis, 463
 2. Ducts, 456
 - (a) Disposal of Gametes, 466
 - (b) Sperm Ducts, 467
 - (c) Oviducts, 470
 3. Apparatus for Effecting Fertilization, 472
 - (a) Fertilization of Animals and Plants Contrasted, 472
 - (b) Holdfast Mechanisms, 472
 - (c) Male Copulatory Organs, 473
 - (d) Female Genitalia, 478
 4. Accessory Glands, 480
 - (a) Originating in the Sperm Duct or Oviduct, 481
 - (b) Originating from the Urogenital Canal, 482
 - (c) Originating in the Integument, 483
 5. Devices for the Care of Eggs and Young, 483
 - (a) Uterus, 483
 - (b) Brood Sacs, 485
 - (c) Nidamental Glands, 485
 - (d) Placenta in Mammals, 486
 6. Degenerate and Rudimentary Organs, 486
- V. Determination and Differentiation of Sex, 489
- VI. Periodicity in Reproduction, 491
- VII. Care of the Young, 494

CHAPTER XVI. Involuntary Regulation (Glands of Internal Secretion) 497

- I. In General, 497
- II. Pharyngeal Glands, 499
 1. Thyroid, 499
 2. Parathyroids, 502
 3. Thymus, 503
 4. Ultimobranchials, 503
- III. Cranial Glands, 504
 1. Pituitary, 504
 - (a) Posterior Lobe, 505
 - (b) Intermediate Lobe, 506
 - (c) Anterior Lobe, 506

- 2. Pineal Body, 507
- IV. Sexual Glands, 508
 - 1. Male Gonads, 508
 - 2. Female Gonads, 508
- V. Abdominal Glands, 509
 - 1. Adrenals, 509
 - 2. The Islands of Langerhans, 512

PART THREE: THE MECHANISM OF MOTION AND LOCOMOTION

CHAPTER XVII. The Skeleton

517

- I. The Rôle of the Skeleton, 517
- II. Joints, 520
- III. Divisions of the Skeleton, 521
- IV. The Main Skeletal Axis, 522
 - 1. The Parts of a Vertebra, 522
 - 2. The Notochord and Its Sheaths, 524
 - 3. The Formation of Vertebral Arches, 525
 - 4. The Embryonic Development of Vertebrae, 526
 - 5. Types of Articulation between Centra, 529
 - 6. History of the Vertebral Column, 531
 - 7. The Entire Backbone, 537
- V. The Thoracic Basket, 539
 - 1. In General, 539
 - 2. Ribs, 542
 - 3. The Sternum, or Breastbone, 548
- VI. Gasteralia, 554
- VII. The Skull, 554
 - 1. The Development of the Brain Case, 555
 - 2. The Splanchnocranium, 562
 - 3. Types of Jaw Suspension, 564
 - 4. Comparative Anatomy of the Skull Bones, 565
 - 5. Middle Ear Ossicles, 582
 - 6. Temporal Fossae, 583
 - 7. Vertebrate Skulls, 584
 - (a) Cyclostomes, 584
 - (b) Elasmobranchs, 585
 - (c) Ganoids, 585
 - (d) Teleosts, 585
 - (e) Stegocephals, 586
 - (f) Modern Amphibians, 586
 - (g) Reptiles, 587
 - (h) Birds, 589
 - (i) Mammals, with Special Reference to Man, 590
- VIII. The Locomotor Skeleton, 600
 - 1. The Necessity for Animal Locomotion, 600
 - 2. Evolution of Locomotor Devices, 601
 - 3. Kinds of Appendages, 603
 - 4. Origin of the Girdles and Appendages, 604
 - 5. Homology and Adaptation, 606
 - 6. The Comparative Anatomy of Girdles, 608

- (a) Girdles in General, 608
- (b) Pelvic Girdle, 609
- (c) Pectoral Girdle, 618
- 7. The Free Appendages, 623
 - (a) Unpaired Fins, 623
 - (b) Lateral Appendages in General, 625
 - (c) Different Pectoral Appendages, 626
 - (d) Different Pelvic Appendages, 633
 - (e) The Human Hand, 640

CHAPTER XVIII. Production of Motion and Locomotion (Muscles)

642

- I. In General, 642
- II. Muscular Activity, 643
- III. Muscles as Tissues, 645
- IV. Muscles as Organs, 646
- V. Embryology of Muscles, 650
- VI. Kinds of Voluntary Muscles, 651
 - 1. Metameric Muscles, 652
 - (1) Axial Muscles, 652
 - (a) Head, 652
 - (b) Trunk, 654
 - (c) Diaphragm, 657
 - (2) Appendicular Muscles, 657
 - (a) Extrinsic Muscles, 657
 - (b) Intrinsic Muscles, 658
 - 2. Branchiomic Muscles, 658
 - 3. Integumental Muscles, 659
- VII. Electric Organs in Fishes, 663

CHAPTER XIX. The Dominating Factor (Nervous System)

665

- I. General Character, 665
- II. The Structural Units, 666
 - 1. Polarity, 667
 - 2. Nerve Fibers and Their Sheaths, 668
 - 3. Microscopic Structure, 669
- III. Reflex Arcs, 670
- IV. Primitive Nervous Systems, 672
- V. The Embryonic Rise of the Nervous System, 674
- VI. Subdivisions of the Nervous System, 676
- VII. The Cord and Spinal Nerves, 677
 - 1. Form of the Cord, 677
 - 2. Extent of the Cord, 678
 - 3. Spinal Nerves, 679
 - (a) Roots, 682
 - (b) Branches, 683
 - (c) Plexuses, 684
 - 4. Development of the Spinal Cord, 685
 - 5. Internal Architecture of the Adult Cord, 688
 - (a) Ascending Sensory Tracts, 690
 - (b) Descending Motor Tracts, 692
 - (c) Association Ground Bundles, 693
 - 6. Comparative Anatomy of the Cord, 695

VIII.	Meninges, 698	
IX.	Brain, 700	
	1. In General, 700	
	2. Comparison of Brain and Cord, 701	
	3. Differentiation of the Brain, 703	
	(a) Constriction, 703	
	(b) Unequal Thickening of the Walls of the Brain, 704	
	(c) Invaginations and Evaginations, 704	
	(d) Bendings, 705	
	4. Ventricles, 706	
	5. General Topography of the Mammalian Brain, 706	
	6. Cerebral Localization, 715	
	7. Craniospinal Nervous Pathways, 718	
	(a) Fasciculi gracilis and cuneatus, 718	
	(b) Spinothalamic Tracts, 719	
	(c) Spinocerebellar Tracts, 719	
	(d) Corticospinal Tracts, 720	
	8. The Comparative Anatomy of the Brain, 723	
	(a) Cyclostomes, 723	
	(b) Elasmobranchs, 725	
	(c) Other Fishes, 727	
	(d) Amphibians, 727	
	(e) Reptiles, 728	
	(f) Birds, 729	
	(g) Mammals, 729	
	9. The Control of the Body by the Brain, 730	
X.	Cranial Nerves, 731	
	1. Terminal Nerve, 737	
	2. Olfactory Nerve, 738	
	3. Optic Nerve, 738	
	4. Eye-Muscle Nerves, 740	
	5. Trigeminal Nerve, 741	
	6. Facial Nerve, 742	
	7. Acoustic Nerve, 742	
	8. Glossopharyngeal Nerve, 743	
	9. Vagus Nerve, 743	
	10. Spinal Accessory Nerve, 744	
	11. Hypoglossal Nerve, 744	
XI.	The Autonomic Nervous System, 744	
	1. Visceral Reflexes, 745	
	2. Autonomic Outflows, 746	
	3. Thoracico-lumbar Division, 748	
	4. Double Autonomic Supply, 750	
	5. Comparative Anatomy of Autonomic System, 751	
CHAPTER XX.	Ports of Entry (Sense Organs)	753
I.	In General, 753	
	1. Stimuli, 754	
	2. Receptors, 754	
	3. Response, 756	
	4. Sensory Range in Animals, 756	
	5. Accessory Structures, 757	

- II. Classification of Receptors, 758
- III. Cutaneous Sense Organs, 760
 - 1. Tangoreceptors, 760
 - 2. Thermoreceptors, 764
 - 3. Algesireceptors, 767
 - 4. Rheoreceptors, 769
- IV. Chemical Sense Organs, 772
 - 1. Olfactoreceptors, 772
 - (a) Odors, 773
 - (b) Structure, 774
 - (c) Accessory Parts, 777
 - (d) Evolution, 778
 - 2. Gustoreceptors, 780
 - (a) Taste Buds, 780
 - (b) Comparative Anatomy, 781
 - (c) Classification, 782
 - 3. Irritoreceptors, 783
- V. Gravity Organs, 784
 - 1. Equilibrium, 784
 - 2. Statoreceptors, 785
 - 3. Semicircular Canals, 786
 - 4. Weber's Organ, 787
- VI. Phonoreceptors, 788
 - 1. The External Ear, 788
 - 2. The Middle Ear, 791
 - 3. The Internal Ear, 795
 - (a) Development of the Membranous Labyrinth, 795
 - (b) Structure in Mammals, 796
 - (c) Physiology of Hearing, 800
 - (d) Comparative Anatomy, 802
- VII. Photoreceptors, 804
 - 1. In General, 804
 - 2. Photoreceptors That Are Not Eyes, 805
 - 3. Eyes, 805
 - (a) Direction Eyes, 805
 - (b) Image-Forming Eyes, 806
 - 4. Human Eyes, 806
 - (a) Development, 808
 - (b) Structure of the Human Eye, 809
 - (c) Accessory Parts, 817
 - 5. Median Eyes, 820
 - 6. Comparative Anatomy, 821
 - (a) Amphioxus, 821
 - (b) Cyclostomes, 821
 - (c) Fishes, 821
 - (d) Amphibians, 824
 - (e) Reptiles, 825
 - (f) Birds, 826
 - (g) Mammals, 828
- VIII. Internal Sense Organs, 830
 - 1. Proprioceptors, 830
 - 2. Interoceptors, 831

PART ONE

THE BACKGROUND

Chordate Characters

I. TYPE STUDY

No one knows how many different kinds of animals there are living today. When Aristotle (384–322 B.C.) wrote the first *History of Animals* he succeeded in rounding up only about 500 species in spite of the fact that Alexander the Great, his famous pupil, gave special instructions to his conquering armies to aid in collecting from the ends of the earth information about foreign animals which his old master so eagerly desired.

Since Aristotle's day explorers have stretched the horizon that then shut in the Mediterranean world, until now even Darkest Africa has been entirely criss-crossed, both poles have been trampled upon, and no considerable corner of the globe anywhere, on land or sea, is left from which authentic tales of animal life have not been brought back.

According to recent estimates upwards of 1,000,000 species of living animals are known to science. Of these probably 65,000 are chordates. In addition there are fossil remains of many more extinct animals that have no living representatives. As long ago as 1890, according to Ward, the manuscript catalogue of known plants at the Kew Gardens weighed over a ton. The inquirer who would be informed about the different kinds of living things might well be appalled at the prospect of passing in review within a single lifetime of study even a tithe of this wealth of animal and plant life.

John Malpet, who in 1567 wrote one of the first "natural histories" in the English language, started his treatise with the hopeful sentence, "Let us begin alphabetically with the adder." There is an easier way out of the situation, however, than by John Malpet's alphabetical method. Even Aristotle recognized in the make-up of animals a *unity of plan* by which they could be placed in natural groups so that acquaintance with a single representative of a group would give a considerable working knowledge of all other kinds within that particular group. Familiarity with the mechanism and behavior of a house cat, for example, gives one a good idea of all other kinds of cats, such as lions, tigers, lynxes, leopards, ocelots, jaguars, wildcats,

pumas, cheetahs, and panthers. In fact much of the fascination that goes with the study of biology lies in recognizing resemblances and differences between various sorts of plants and animals.

Although the number of kinds of plants and animals is very great, the different general types or plans of structure are relatively few, so that the student, by using the *type-study method* of sampling, may set out confidently and with a brave heart upon the ambitious quest of intellectually conquering all creation.

Limiting the survey solely to animal life, a list of the chief types of animals comprises: PROTOZOA, COELENTERATA, PLATYHELMINTHES, NEMATHELMINTHES, ANNELIDA, ARTHROPODA, MOLLUSCA, ECHINODERMATA, and CHORDATA.

II. COMPARATIVE STUDY

Of all animal types the *chordate type* is of most immediate interest, since it includes man. Many of the riddles connected with that much studied animal find their solution in the lower forms.

For instance, the *parietal body*, a conical projection about the size of a cherry stone, is buried between the lobes of the human brain. Its origin and



Fig. 1. A primitive New Zealand lizard, *Sphenodon*. (After Berg.)

use baffled anatomists for centuries until Baldwin Spencer in 1886 dissected a New Zealand lizard, *Sphenodon* (Fig. 1), by some called a "living fossil." He discovered that in the chordate type, the "parietal body," or a part arising from it, is simply a de-

generate median eye since in this curious primitive reptile it reaches, with retina and nerve complete, all the way to a transparent window in the roof of the skull and, in early life at least, may function as a third eye.

It is entirely true that often more may be learned of human development and structure by the intelligent examination of a dogfish, or some other lowly vertebrate, than by the direct study of the human body itself. This is due not so much to the greater availability of lower animals for dissection and experimentation, as to the fact that they furnish sidelight stages through which the human body has passed in arriving at its present degree of complexity, and thus give a clue for interpreting the why and wherefore of the "fearfully and wonderfully made" human mechanism. Herein lies the value of the study of *comparative biology*.

The indirect path has thus been often the shortest cut to unexpected attainment in the history of science. Inquisitive Ben Franklin, out in the

thunder-storm with his key and kite, took the first step towards harnessing electricity; the Frenchman Daguerre, trying to discover some way to clean tarnished silver, blazed a path which has become a broad highway in photography and the colossal motion-picture industry; Alexander Graham Bell, attempting to aid the deaf to hear, led to the invention of the telephone; Joseph Cushman, with insatiable curiosity about the variety of forms of microscopic shelled protozoans, hit upon a way to tell those who bore for oil when they were on the right track; while Pasteur, a thinking chemist interested primarily in the apparently remote subject of the shape of crystals, laid firm foundations for the far-reaching developments of bacteriology and modern medicine.

When such facts as these are recalled, nothing about the structure or activities of any animal, however familiar or strange, becomes insignificant or trivial to the seeker after truth concerning man.

III. ESSENTIAL FEATURES OF EVERY ANIMAL TYPE

Every form of life, whether plant or animal, must possess machinery of some sort for accomplishing two fundamental processes, namely, metabolism and reproduction.

Metabolism includes all activities that concern the upkeep of the individual, such as the intake of energy by way of food, its release in the form of action which constitutes "living," and the disposal of waste products incident thereto.

Reproduction provides for the continuation of the species upon the earth, often at the cost of the individual life.

The former function may be designated as selfish and egoistic, the latter as unselfish and altruistic.

A typical insect, for example, is made up of three easily distinguishable regions, in order of relative importance, the abdomen, thorax, and head (Fig. 2). In the large *abdomen* is lodged the principal machinery for metabolism and reproduction, that is, most of the digestive apparatus, the respiratory, excretory, and circulatory machinery, and the reproductive organs.

The *thorax* is devoted primarily to locomotion, furnished as it is with three pairs of legs and usually with two pairs of wings together with the muscles necessary to work them, and is thus enabled to transport the



Fig. 2. A typical insect, showing the *abdomen*, all important as the chief region of metabolism and reproduction, the locomotor *thorax*, and the directive *head*.

important abdomen to places where it can selfishly procure energy-producing food and unselfishly provide for the next generation. Finally, there is the *head*, with its battery of directive sense organs and a controlling brain, which tells the thorax and abdomen where to go and what to do upon arrival. Many animals get along comfortably without a head or locomotor devices, but none can dispense with the all-important abdomen or something corresponding to it. Even in man that crowning glory, the head, which he is quite apt to regard as important, as well as the locomotor legs, becomes quite subsidiary when the trunk, that corresponds to the insect's abdomen, sends out the imperious call of hunger or of sex.

The function of metabolism is usually accomplished in a different way by animals than it is in plants, with the result that most plants remain stationary, while most animals move about. The reason for this difference lies in the fact that green plants possess the power, in the presence of sunlight, of building up their foods out of universally distributed materials, such as carbon dioxide in the air, water, and various inorganic compounds in the soil. No animal can do this, so it comes about that all animals must find their energy, either directly or indirectly, in the stored supply already captured by green plants from the sun. This is why most animals are forever fated, like the Wandering Jew, to be travelers, a condition which necessitates in animal types some adequate device for locomotion, and consequently an accompanying directive sensory equipment. The fact that certain animals like oysters and corals are sedentary is the exception to the rule. "Their strength is to sit still." Even in the case of these animals the indirect dependence on green plants is quite as complete as among locomotor forms, since they feed upon microscopic green plants that form the floating meadows of the ocean, and in consequence have developed secondary devices for bringing this floating food to them. Most animals digest their food in an *alimentary canal*, which begins in a *mouth* near the anterior end of the body and terminates posteriorly in an *anus*.

IV. SYMMETRY

The science of the form and shape of organisms is called *Morphology*, a term coined by the many-sided Goethe in 1817. It is closely related to the mathematical science of *Solid Geometry*, with the difference that the mathematician has little occasion to inquire why one figure is a cube and another a sphere except to determine the relation of the different dimensions to each other, while the biologist is constantly being challenged to explain *why* each organism is shaped as it is, in relation to the particular life that it leads. Moreover, the shapes and forms with which the geometrician deals

are arbitrary creations of the human mind, not particularly related to the environment, having no modifying past and no forward look to a future in which modifications may take place. The forms of animals and plants which a biologist considers are the products of an actual historical sequence that has taken place, of ancestral shapes that have in succession all left their determining impress.

There are no animals with less than three dimensions, although some of the lower forms are so small and thin as to necessitate very delicate instruments to determine their length, breadth, and thickness.

Three fundamental shapes and forms are recognized and, as a result, three general types of symmetry, namely, spherical, radial, and bilateral. Each of these types may be camouflaged in various ways by secondary modifying qualifications.

Spherical symmetry in organisms is rare. It is to be found only among microscopic animals, such as the Heliozoa, or "sun animalcules" of the protozoan type which float without contact with anything solid, surrounded by water on all sides. Many floating animals, on the other hand, become attached, during a part of their life at least, and lead a sedentary plantlike existence. Such anchored animals are usually headless, and frequently develop a crown of radiating arms or tentacles that enable them to reach out in every direction to explore as far as possible their immediate neighborhood. This headless plan is the *radial type of symmetry*, which in general is characteristic of trees and other stationary plants, as well as of attached or sessile animals, whose food is brought to them floating in water. In all of these organisms the body possesses polarity, being organized along a longitudinal axis with an attached end and a free end.

On land, where food does not float in a transporting medium, animals have to travel to obtain it when they are hungry. This has made necessary a directive head. Although a head end is characteristic of certain water animals such as fishes, it becomes an absolute necessity for locomotor land animals. Whenever an animal moves persistently in one direction with reference to its own body, in other words whenever a true head end is established, *bilateral symmetry* results, and a stagnant life of watchful waiting ceases. With the appearance of this type of symmetry animals usually develop the habit of keeping one particular side of the body either in contact with the substrate or facing downwards. This undersurface is the *ventral* side of the animal, while the upper surface is the *dorsal* side. The body presenting this type of symmetry may be divided into halves by means of three planes which can be arranged with reference to length, breadth, and thickness.

In radial symmetry, on the other hand, the number of planes dividing the animal into similar halves is practically infinite, like the number of ways in which a cylinder may be split lengthwise into two equal parts.

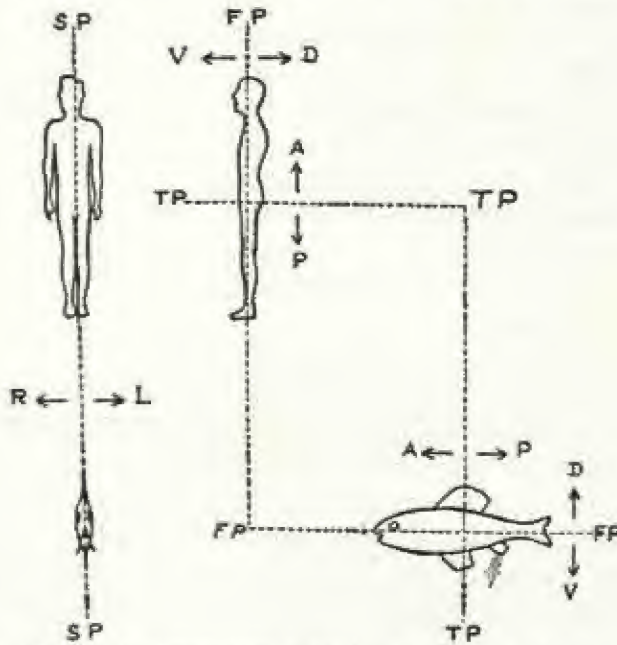


Fig. 3. The planes of symmetry in bilaterally symmetrical animals, with the resulting regions. S.P., sagittal plane; F.P., frontal plane; T.P., transverse plane; R, right; L, left; D, dorsal; V, ventral; A, anterior; P, posterior.

The three planes (Fig. 3) bisecting length, breadth, and thickness divide any bilaterally symmetrical animal into definite regions, very useful as landmarks in description, as follows:

Sagittal plane dividing the body into *right* and *left* halves, mirror images of one another;

Transverse plane dividing the body into *anterior* and *posterior* halves;

Frontal plane dividing the body into *dorsal* and *ventral* halves.

The sagittal and frontal planes are so named because of certain sutures in the human skull with which they coincide. It is obvious that upright man moves forward with the ventral body-half in front, instead of the anterior body-half, because he is a bilaterally symmetrical animal tipped up on end.

Although the comparative anatomist uses the above terms, the student of human anatomy sometimes uses a different set. The head-end may be known as the *superior* portion in man, while the lower part of the body is

the *inferior* portion. The terms *anterior* and *posterior* are then used as the synonyms of "ventral" and "dorsal," respectively, of comparative anatomy.

V. METAMERISM

The body of an annelid worm, an arthropod, or an embryonic chordate consists, in basic plan, of a series of similar, repeated divisions (*metameres* or *segments*) arranged one behind the other. An adult annelid (e.g., *Nereis*) very closely approximates this basic plan, with the the metameres clearly marked off externally. Each metamere, except the first and last, possesses a pair of appendages. Internally, at the level of each external constriction, there is found a cross-partition (*septum*). Other internal structures, such as nephridia, tend to be repeated in each metamere. Chordates, however, never have external constrictions, although most of them exhibit internal segmentation of a number of embryonic organs, for example, the skeletal muscles. The axial skeleton and the nervous system show a modified metameric organization.

VI. COELOM

The chordates, in common with annelids, echinoderms, and some other invertebrate phyla, possess a coelom (the so-called true body cavity), lined with mesodermal tissue and lying between the digestive tract and the body wall. Thus great freedom is permitted for the development and activity of embryonic organs as well as for the movement of such adult parts as the heart, stomach and intestine.

VII. CHORDATE CHARACTERISTICS

The backboneed animals (*Vertebrata*), together with a few closely related animals which do not possess a backbone, are ordinarily included in the Phylum *Chordata*. In the preceding sections certain chordate features, also commonly possessed by members of other animal phyla, have been considered. These *primitive characters* of chordates include: (1) reproductive glands; (2) alimentary canal; (3) polarity; (4) bilateral symmetry; (5) metamerism; and (6) coelom.

Chordates also possess certain other features, which distinguish them from all other animals. The chief *diagnostic characters* of chordates are the following:

1. Notochord

During the embryonic development of every chordate there appears a supporting rod, the *notochord*, which lies immediately dorsal to the digestive

tract. In some chordates this structure persists throughout life; in others it is partially or completely replaced by a skull and a "backbone" made up of separate bony elements, or vertebrae, as the name "vertebrate" indicates. Essentially the notochord consists of a tough connective tissue sheath in which soft cells are packed so tightly that the whole structure possesses a certain turgor, somewhat like that when sausage meat is crowded into a casing (Fig. 98).

2. Dorsal, Hollow, Central Nervous System

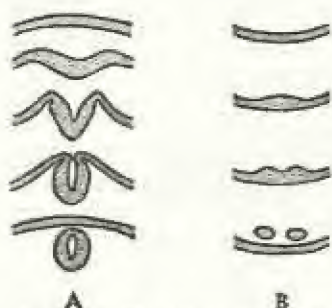


Fig. 4. Successive stages in the migration of outside tissues to the inside. A, by invagination; B, by delamination.

The chordate nervous system develops on the dorsal side of the body by a process known as invagination (Fig. 4). In this structure, even in adult animals, there is a cavity which is continuous from near the anterior end of the brain to the posterior end of the nerve cord. The central nervous system of non-chordates, on the other hand, is formed on the ventral side of the body and is solid. In the vertebrate members of the chordate phylum, the anterior end of the central nervous system is much enlarged into a brain with which there are associated three pairs of major sense organs: olfactory (nose); optic (eyes); and otic (ears).

3. Pharyngeal Breathing Device

Fishes have several porthole-like passage-ways, or gill slits, penetrating through the lateral walls of the food tube on either side of its anterior end. Within these gill slits in water-dwelling chordates hang feathery tufts of capillaries, or gills, which rob the circulating water of some of its dissolved air, thus accomplishing the function of breathing.

Gill slits, or traces of them, are present, at least in embryonic life, in all chordates, whether dwelling in water or out of it, and even in reptiles, birds, or mammals which never breathe by means of gills. Whenever breathing is accomplished by lungs, such organs develop as side alleys from this same anterior pharyngeal region of the food tube where the gills originate. No non-chordate breathes in this way, although many kinds of animals employ "gills" of various sorts. *Pharyngeal gills* and *gill slits*, or traces of them, are peculiar to chordates.

These first three chordate characteristics are present at some time during the life of every individual of the chordate phylum.

4. Ventral Heart

The heart, which is the headquarters of the circulatory system, is ventrally located in chordates. In other animals, when a heart is present, it is on the dorsal side of the body.

5. Closed Blood System

In chordates the blood courses through a continuous system of tubes from heart, to arteries, to capillaries in the various tissues, to veins, and back to the heart again. Most non-chordates, on the other hand, have an open blood system, that is, one in which the blood may pass freely back and forth between the blood vessels and surrounding spaces or sinuses. The contrast is remotely like that between the waterworks of a modern city with water and sewage confined to pipes and mains, and the open ponds and streams of the countryside.

6. Hepatic Portal System

Although venous systems, beginning in capillaries in the tissues of the body, ordinarily terminate at the heart, there are places where veins not only begin but also end in capillaries. Such a group of veins is known as a portal system. In most chordates, the food-laden blood from the digestive tract passes through a strainer-like capillary network, the liver, before it arrives at the heart to be sent over the hungry body. The group of veins beginning in capillaries in the digestive tract and ending in hepatic (*hepat-*, liver) capillaries is known as the *hepatic portal system*.

Although other animals have organs that are called "livers" by courtesy, only chordates have a true liver, or clearing house, where the strained blood is reorganized by addition and subtraction of various substances before being distributed to different parts of the body.

7. A Post-Anal Tail

A true tail may be defined as a continuation of the body axis posterior to the anal exit of the food tube. That part of a lobster, for example, which is sometimes erroneously called the "tail," is not a true tail at all, but the abdomen, since the anus opens at the end of it. Each vertebrate has a true tail, either throughout life or embryonically and ancestrally. Even tailless man has in his early fetal stages an unmistakable tail (Fig. 5), and there are numerous well-authenticated

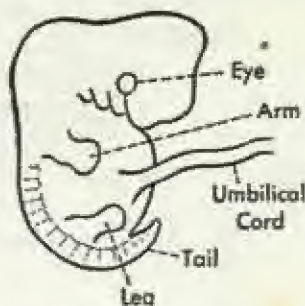


Fig. 5. Lateral view of a young human embryo showing tail. (After Ecker.)

cases reported in medical literature of human tails that persist beyond embryonic life.

8. Red Blood Cells

The red respiratory pigment of the blood may be dissolved in the liquid part of the blood or may be confined in red blood cells. In the chordates the pigment is always in cells. In non-chordates it is usually in the plasma, but in a number of species, scattered among various invertebrate phyla, the red pigment is in cells. Among the non-chordates possessing red blood cells are: *Arca*, a bivalve mollusc; *Glycera*, a polychaete annelid; and *Thyone*, a sea cucumber of the echinoderm phylum. These particular examples are chosen because they are relatively common animals representative of three different phyla. No evolutionary significance is to be attached to the occurrence of this chordate feature in widely scattered species of invertebrates.

VIII. COMPARATIVE DIAGRAMS OF CHORDATES AND NON-CHORDATES

A visualized diagrammatic summary of some of the outstanding points of contrast between a generalized chordate and a corresponding non-chordate is presented in Fig. 6.

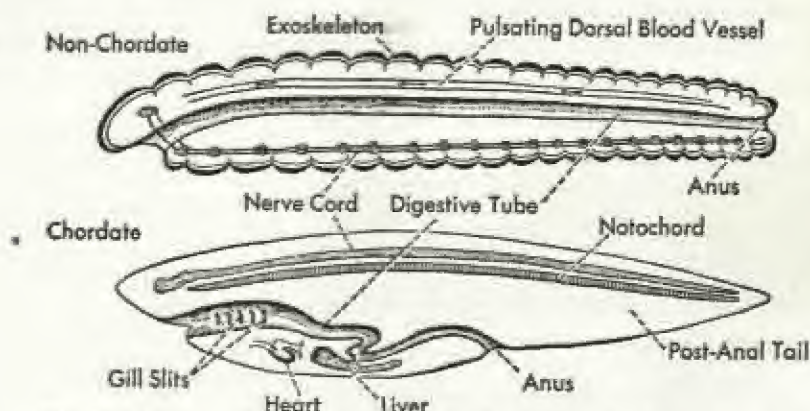


Fig. 6. Comparative diagrams of the fundamental plans of a non-chordate (above) and a chordate (below).

Kinds of Vertebrates

I. TAXONOMY

In nature one encounters all sorts of different animals intermingling without any apparent law or order. It is necessary, therefore, with all this diversity to invent some workable system that will bring cosmos out of chaos and make "type study" possible, otherwise confusion is inevitable and the effort to become familiar with all living things is hopeless.

First of all it is essential to become acquainted with as many kinds of animals as possible, not alone through pictures and names of animals that live so dreary a life in textbooks, but through actual acquaintance with real animals. Taxonomy, or classification of animals and plants, is dull and without point until one has gained a personal acquaintance with enough organisms to make it worth while. This chapter consequently should be referred to only as a last resort after various kinds of animals encountered begin to be familiar and interesting, and there is something to classify.

Classifications, it should be noted, are more than arbitrary sets of pigeon-holes labeled with forbidding technical names, in which to file away and forget our animal associates, for they involve a compact summary of knowledge concerning the origin and derivation of different organisms.

In mentally putting together animals of a kind, the ideal criterion to employ is *hereditary relationship* rather than *external resemblance*. It is the particular province of *comparative morphology* to discover such relationships. A whale, for example, is properly classified with mammals rather than with fishes, which it superficially resembles and with which it associates, because its common origin with animals of the mammalian type is indicated by the fundamental fact that, along with many other mammalian peculiarities, its young are born alive and fed at first upon milk.

Superficial features, like the transparency of many open-sea forms as diverse as jellyfish, shrimp, pteropod mollusks, worms, and larval fishes, or the power of aerial flight on the part of such plainly unrelated creatures as birds, bees, and bats, tell us *where the animal has been spending its life*,

while animals as unlike in appearance as whales and bats, herons and hummingbirds, eels and flatfishes, butterflies and bedbugs, or lobsters and barnacles, belong together in any scientific classification, because each pair is built on the same fundamental plan and has a blood relationship, one with the other.

Owing to the incompleteness of our present knowledge about the evolution and blood relationship of animals there is still considerable uncertainty and controversy among taxonomists as to "who's who" in any classification, and as a result several different arrangements are current in books dealing with the subject. The same scientist, as his store of knowledge grows, may change his original classification. For instance, David Starr Jordan, America's foremost authority on the group of fishes, in a classification of North American fishes (Jordan and Copeland) in 1876, named 670 species. Twenty-two years later, in 1898, he published a new list (Jordan and Everman) including in it only 585 species in spite of the fact that meanwhile 130 new species had been brought to light.

Ward refers to two kinds of taxonomists, namely, "hair-splitters" and "lumpers," and we are free to choose between them, for there is no indisputable hard and fast classification that we are bound to accept to the exclusion of all others.

Although opinions differ with regard to the details of systems of classification, there is substantial agreement with regard to the sequence of the following groups in which

like INDIVIDUALS make up SPECIES		
" SPECIES	" "	GENERA
" GENERA	" "	FAMILIES
" FAMILIES	" "	ORDERS
" ORDERS	" "	CLASSES
" CLASSES	" "	PHYLA
" PHYLA	" "	KINGDOMS

The manner of employing these groups may be illustrated by classifying a particular individual house cat, named "Tom" (Fig. 7). It will be seen that this cat finds itself admitted successively into more and more inclusive groups, until finally, as a member of the vast animal kingdom, it has quite lost its individual importance. If now we retrace our steps in the diagram from the all-inclusive *animal kingdom*, we see the individuality of "Tom" gradually emerging until it may be concluded that this cat at least possesses not only the general characteristics listed in the preceding chapter as vertebrate characteristics, but also that it has the special equipment that makes

it a mammal and a carnivore, like the lions, tigers, and their kind, and last of all it has an individuality that distinguishes it from all other domestic cats which are well known in their several households.

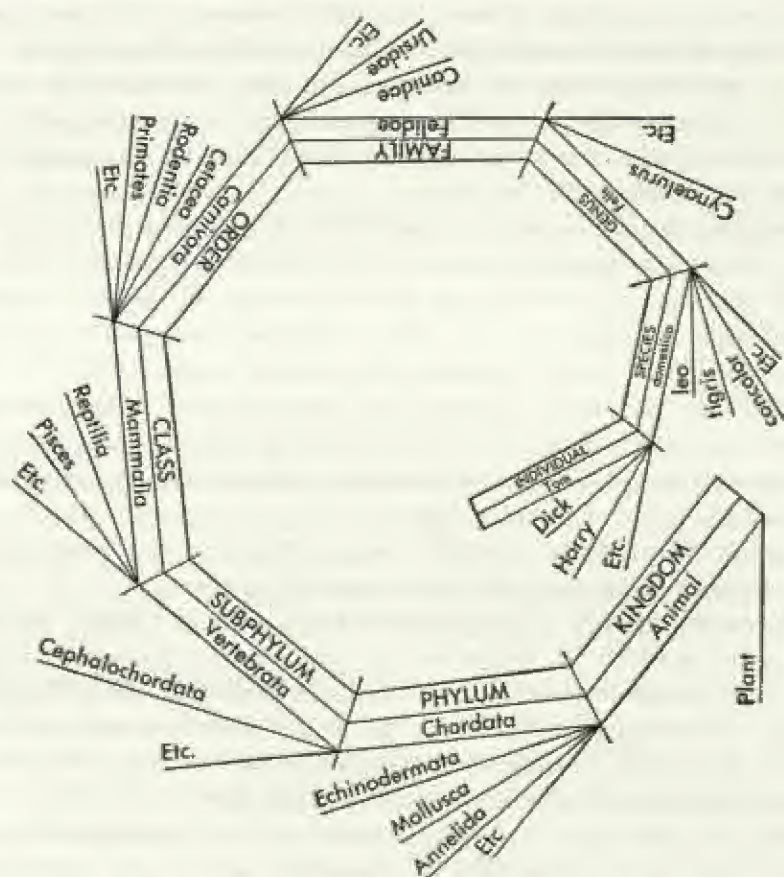


Fig. 7. The taxonomy of a cat named "Tom."

Although Darwin, who wrote *The Origin of Species*, was unable to define just what are the limits of a species, which is a concept that has no exact counterpart in nature, he nevertheless made it clear that a species is a real entity that outlives the separate individuals composing it. The species concept of "cats" will remain long after the individual *Tom* has lived out the traditional nine lives of cats and turned to dust.

II. SCIENTIFIC NAMES

In a serious study of animals it is necessary to employ *scientific names*. Common names which, like nicknames or pet names, may have only a

limited local application, do not invariably lead to accuracy in identification. Sailors are not initiated into life on the deep until they can command a vocabulary of technical terms that are strange to the landsman. Even baseball fans have a lingo all their own which corresponds to the scientific terminology that the biologist finds not only useful but indispensable.

It is noteworthy that the first recorded task ever done by man is reported in Genesis 2:20, "and Adam gave names to all cattle, and to the fowl of the air, and to every living beast of the field." So Taxonomy is the first and most ancient of all sciences!

The great Swedish naturalist Linné (1707-1778), who introduced into biology a complete system of nomenclature, thereby raised biology from an inferior position as an adjunct of medicine to the dignity of a separate science simply by paving the way with an adequate biological terminology. He employed Latin mostly in making his scientific names. This was advisable since Latin is a "dead language," no longer subjected to the changes in form and meaning to which any spoken language is liable. Latin, moreover, came the nearest to being the fundamental universal language of educated peoples of all tongues. Faithfully christening all the animals and plants known to science in his day with a scientific name, Linné even included himself so that he is generally known by the Latin name of *Linnaeus*.

A complete scientific name consists of three parts, as follows: the name of the *genus* to which the animal belongs; the name of the *species*; and the name of the *namer*, or godfather, who does the christening. In all languages, therefore, *Felis domestica* Linn. is the proper scientific name for every common house cat, because these cats belong to the genus *Felis*, to the species *domestica*, and were so named in the first place by Linné.

When the same kind of an animal is given two or more scientific names independently and unawaredly, as frequently occurs, the confusion is remedied by adopting the first name assigned, if it can be determined, in accordance with the "law of priority."

In any scientific name the genus is invariably written with a capital letter and the species with a small letter, although it is permissible sometimes, when a species is named in honor of a person or place, to employ a capital letter. Both generic and specific names are always printed in italics. According to common practice the name of the namer, which is principally useful in determining priority in doubtful cases, is frequently omitted.

Every student of biology who sets out in earnest to excel, must conquer any childish aversion he may have for the imaginary terrors of unfamiliar scientific names and should acquire, as soon as possible, facility in the use of these indispensable tools of his trade.

III. A ROLL CALL OF CHORDATES

Before proceeding further with a consideration of the comparative biology of the vertebrates, it is necessary to pass in brief review the different kinds of vertebrates between which comparisons are to be made.

The phylum Chordata may be lined up in the following array:

Subphylum I	HEMICHORDATA
Subphylum II	UROCHORDATA
Subphylum III	CEPHALOCHORDATA
Subphylum IV	VERTEBRATA (CRANIATA)
Class I	Cyclostomata
Class II	Pisces
Class III	Amphibia
Class IV	Reptilia
Class V	Aves
Class VI	Mammalia

A. BORDERLINE CHORDATES

There are certain animals which have difficulties in qualifying in all particulars as vertebrates but are, nevertheless, classified as chordates. These interesting connecting links between vertebrates and invertebrates may be called "borderline chordates," or Protochordates. They comprise three subphyla, namely: HEMICHORDATA, UROCHORDATA, and CEPHALOCHORDATA.

1. Subphylum HEMICHORDATA

Dolichoglossus kowalevskyi, found on the Atlantic coast (Fig. 8), may be taken as a representative of the Hemichordata, of which there are only a few genera. This small, fragile, wormlike animal has no common name, because it is not commonly known, an additional reason for resorting to the use of a scientific name. Its body is divided into three general regions: (1) a *proboscis* used to push aside the sand as the animal works its way along; (2) a short *collar*; and (3) the *trunk*, making up by far the greater part of the body. It lives buried in mud at various localities along the Atlantic seashore where at low tide its burrows may be identified by peculiar coiled piles of castings similar to those deposited by earthworms (Fig. 9).

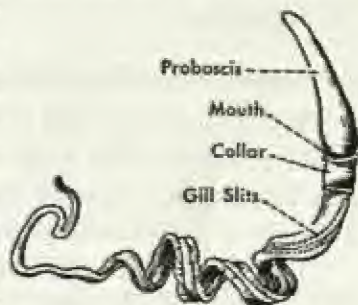


Fig. 8. *Dolichoglossus*, a borderline chordate. (After Bateson.)

The hemichord is of special interest to the biologist since, unlike any true worm, it has the three major chordate characteristics. Numerous, U-shaped,

pharyngeal gill slits are present in the anterior trunk region. There is a dorsal nerve cord which usually possesses merely a few isolated small cavities in the collar region only. A ventral nerve strand, more or less comparable

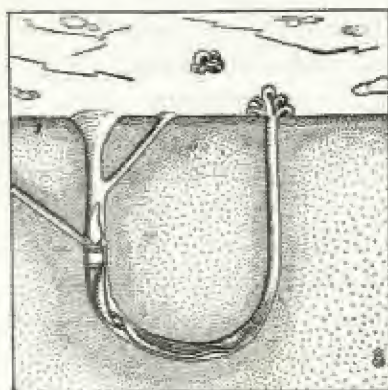


Fig. 9. *Dolichoglossus* in its tube 30-60 cm deep in sand. (After Stiasny.)

to that of invertebrates, is connected with the dorsal cord by a nerve ring in the collar region. Finally, an outgrowth from the dorsal side of the digestive tract of the collar region, extending forward into the proboscis, may represent the notochord.

Although hemichordates are wormlike in many structural details, the few chordate features just mentioned suffice to indicate their problematical position between invertebrates and vertebrates.

The Tornaria larvae of hemichords resemble corresponding stages of echinoderms so much that the Tornaria was for a long time thought to belong to some member of that phylum. The similarities of these two larval types have served as a basis for considering the echinoderms as the invertebrate group most closely related to the chordates.

Different species are found widespread in similar habitats the world over. For example, in 1896 during the Harriman Expedition, Dr. W. E. Ritter, an authority on this group of primitive animals, discovered among other kinds along the shore of Alaska a new genus of hemichords, probably the most primitive of them all, which he christened *Harrimania* in honor of the expedition.

2. Subphylum UROCHORDATA

The Urochordata are *tunicates* or *ascidians*, so called not only from a peculiar baglike outer lifeless envelope, or "tunic," with two openings but also because their general appearance suggests an "askidion," the Greek name for a primitive wine sac made of goatskin.

These degenerate representatives of the chordates are all marine organisms, living for the most part a sedentary life. *Molgula manhattensis*, DeKay, a common "sea squirt" found along the Atlantic shore attached to piles and other objects, may be taken as a typical species.

The only structures conspicuous externally are two projections each of which bears a terminal opening (Fig. 10). Water is continuously taken into the body through one of these openings (the *mouth*) and discharged

through the other (the *atriopore*). Internally, the mouth leads into a *pharynx*, an enlargement which occupies a considerable portion of the body cavity of the animal. The pharynx is permeated by numerous *gill slits* which open into the *atrial cavity*, a space almost completely surrounding the pharynx and opening to the outside through the *atriopore*. Beyond the pharynx the digestive tract continues for a short distance as a small tube, which usually makes one loop and then opens into the atrial cavity. Located on the dorsal side of the pharynx, between mouth and *atriopore* regions, is a solid mass of nerve tissue, the *neural ganglion*. There is no notochord. Thus only one of the three main chordate characteristics is present in the adult.

It is the early life of the tunicate, however, that gives the real clue to its unmistakable relationship to true chordates, which it so little resembles when superficially examined. The egg develops into a free-swimming tadpole-like larva (Fig. 11), showing in its locomotor tail an unmistakable notochord and a single tubular dorsal nerve cord. This is the reason for the name of the group, "Urochordata" (*uro*, tail; *chorda*, notochord).

After the larva swims about for a time and increases in size, it settles down on a suitable support and enters upon its lifetime of stationary existence. The tail, no longer needed for locomotion, is absorbed into other tissues of the body. The central nervous system, reduced to a simple dorsal ganglion, permits only an over-all contraction of the entire body in response to any stimulation. The pharynx, on the other hand, enlarges greatly and becomes the only one of the three chief chordate characteristics to remain well developed in the adult. The tunicate thus sacrifices most of its birthright of chordate characteristics, that is, notochord and tubular nerve cord.

Some tunicates as the result of budding are colonial in habit, living connected together in more or less dependence upon each other, a state of affairs not uncommon among invertebrates but which does not occur elsewhere among chordates. The compound or colonial manner of life is shown,

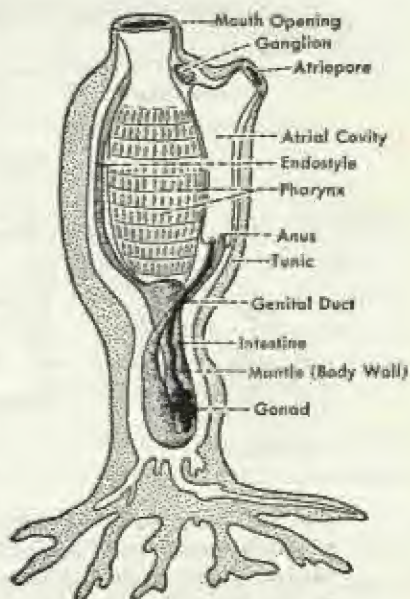


Fig. 10. Internal organization of a simple tunicate. (After Haller.)

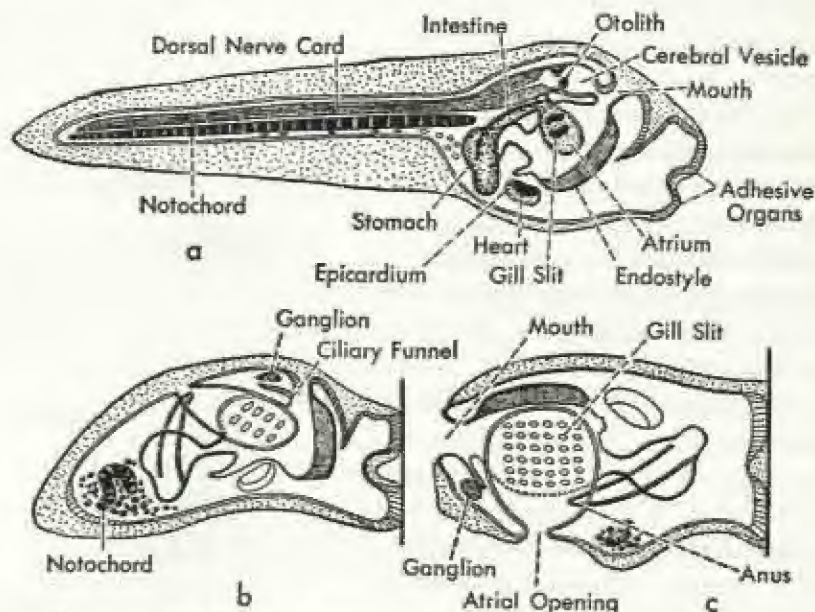


Fig. 11. Diagrams of the metamorphosis of a tunicate larva. a, at time of attachment; b, at mid-point of metamorphosis; c, metamorphosis completed. (From Hegner, *College Zoology*, copyright 1942, by permission of The Macmillan Company, publishers.)

for example, by *Botryllus* (Fig. 12), a small tunicate that grows in starlike slippery patches over the surface of seaweeds floating in the shallow waters of the seashore. The incurrent openings of the several individuals in the

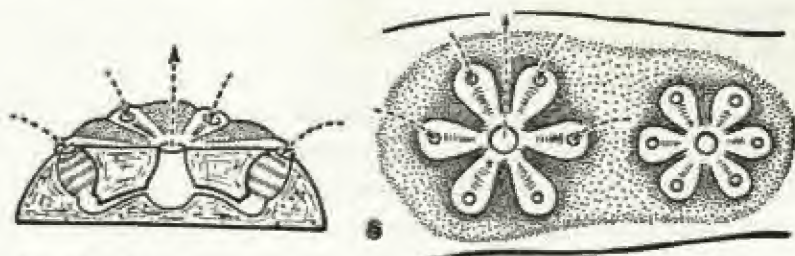


Fig. 12. *Botryllus*, a compound tunicate. Left, section of a colony, showing the common exit; Right, surface view of two colonies surrounded by a gelatinous mass, growing upon the flat surface of a bit of seaweed.

colony are separate and arranged in a circle around a common excurrent opening.

Other colonial tunicates, such as the beautiful transparent "chain salpas," are pelagic, or free-swimming in habit, forming elongated rafts of

barrel-shaped glassy-clear individuals which float near the surface of the ocean, usually many miles off shore.

Most primitive of all these humble cousins of the vertebrates are the microscopic Appendicularia, tiny ghostlike creatures of the vast ocean waters, that live a life of complete freedom and do not relapse, like other tunicates, into unambitious sedentary degeneration, but remain larval "tadpoles" throughout life. Animals such as these, which never "grow up" but become sexually mature while in the larval stage, are said to be *paedogenic*.

3. Subphylum CEPHALOCHORDATA

The Cephalochordata, so named because they have a notochord extending into the head region, include only two genera, *Branchiostoma* and *Asymmetron*. This subphylum is also called Acraniota because of the absence of a cranium, or brain case. If these animals had a cranium they would have nothing to put in it, for they are brainless little creatures whose nerve cord fails to enlarge at its anterior end into anything like a brain.

Amphioxus (*Branchiostoma*), the most widely known member of the group, has had enough written about it to fill more than one ponderous tome. For a century or more it was looked upon as a most primitive chordate, a "fish in the making," illustrating the beginnings of many great things. More recent work has cast considerable doubt upon this point of view, especially when some of the highly specialized features of *amphioxus* are taken into consideration. Yet this animal has apparently retained a great many relatively simple features, despite the fact that it has probably evolved a long way from the actual ancestors of the chordates. If we direct our attention away from the few specialized structures of *amphioxus* and toward its many important basic features, as we must always do in any type study, we find that this animal shows us the chordate plan reduced to almost its lowest terms.

Amphioxus dwells in the shallow waters of tropical and semi-tropical seas in locations as far apart as the Bay of Naples, the coast of Peru, Japan, the Indian Ocean, California, the Philippines, West Indies, Australia, North Carolina, Hawaii, Maldivé Islands, and China. This wide distribution suggests the great antiquity of the type which, in spite of its restricted means of locomotion, has had time to spread to the uttermost tropical corners of the earth.

Off the coast of southern China, north of the Island of Amoy, *amphioxus* is so abundant that it forms an important food fishery which has been worked by the Chinese for centuries. Professor S. F. Light writes in *Science* for July 27, 1923: "Here on this little strip of coast about 400 fishermen,

using 200 small boats, are engaged for from two to four hours on the ebb tide of every calm day during the nine months from August to April of each year in dredging for amphioxus for the market. The catch averages about 2600 pounds, well over a ton for each calm day during the nine months of the fishing season and a total of hundreds of tons of amphioxus are taken during the year!"

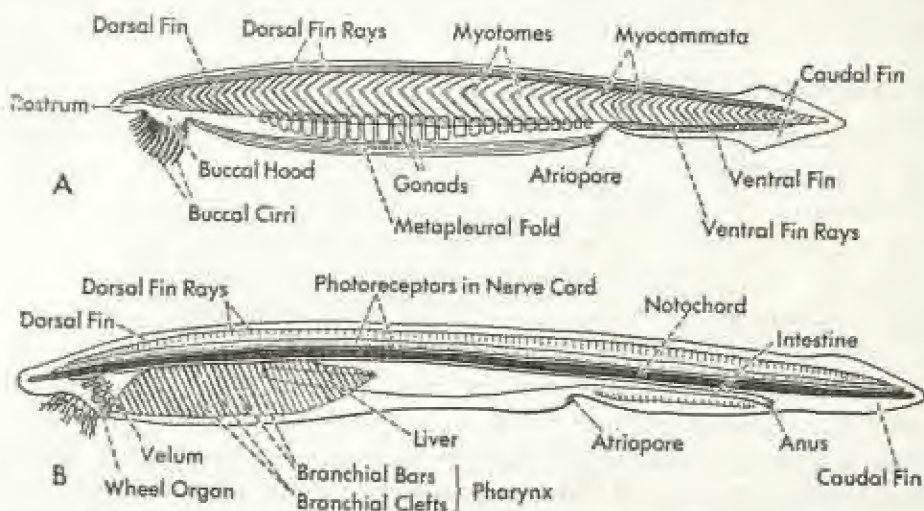


Fig. 13. Diagrams of amphioxus. A, side view of the entire animal; B, side view showing internal features. (A, after Kirkaldy.)

It is not as a source of Chinese food, however, that the chief interest in amphioxus lies, but because in its development and structure this little animal points the way to the rise of the complicated conditions found in higher vertebrates. It will be necessary later on, when tracing the origin of various vertebrate organs, to go back repeatedly to the stage presented by amphioxus.

Amphioxus, or the "lancelet" as it is commonly called, is an elongated, semi-transparent, fishlike animal, two or three inches in length when fully grown, and somewhat pointed at either end, as its Greek name (*amphi*, both; *oxus*, sharp) indicates. In habit it is largely sedentary, lying buried in the sandy bottoms with its anterior end projecting. It is a poor swimmer, coming to rest by lying on its side when not burrowing into the sand.

At the anterior end, guarding the mouth, is a circle of bristle-like *cirri* attached to the edge of the *buccal funnel* within which is a whirlpool of cilia, the "*wheel organ*," which helps to direct the microscopic food into the mouth (Fig. 13).

Running along the entire dorsal side of the body, then around the tail end and forward on the ventral side is a continuous *median fin*. This fold of the skin, as it passes around the tail end, expands to form a conspicuous *caudal fin*. As the fold reaches the region of the atrial pore, anterior to the anal opening, it divides like a letter Y, and extends forward in ventro-lateral folds on either side of the body. It is out of persisting parts of similar folds, which are laid down temporarily in the embryos of fishes, that fins are formed (Fig. 14).

Of all known lower chordates, amphioxus shows the best development of diagnostic chordate features. Extending the entire length of the body just dorsal to the digestive tract is a *notochord* (Fig. 15). Above the latter is the *dorsal, hollow central nervous system* which, instead of enlarging anteriorly into a brain, actually is more slender near its anterior end than throughout most of its length. Not far from the *mouth*, the digestive tract becomes greatly en-



Fig. 14. Diagrams of the phylogenetic development of unpaired and paired fins according to the fin-fold theory. A, primitive stage, with continuous fins; B, differentiated stage, with fins remaining after partial absorption of the primitive continuous fins. (After Wiedersheim.)



Fig. 15. Cross section of amphioxus through posterior part of pharynx.

larged into a *pharynx*, the wall of which is penetrated by 26 pairs of long, narrow *gill slits*. Beyond the pharynx an uncoiled *intestine* of small diameter leads to an *anus* located on the left side of the mid-ventral region a short distance from the posterior end of the body. Thus, a *post-anal tail* is present.

Cilia of the wheel organ and pharyngeal wall ordinarily maintain a continuous flow of water through the pharynx and gill slits. This water not only acts as a respiratory current but also brings in numerous small organisms which serve as food.

Extending the entire length of the pharynx are two grooves, a ventral *endostyle* and a dorsal *epipharyngeal groove*. Both are heavily ciliated. In the endostyle numerous glandular cells secrete mucus which is carried anteriorly by ciliary action. Other cilia transport small streams of the mucus dorsally along the inner surfaces of the gill-bars into the epipharyngeal groove. In the latter the cilia carry the mucus posteriorly into the intestine. Microscopic organisms brought into the body by the so-called respiratory current are trapped by the mucus and eventually carried into the intestine. The lining of the latter is also ciliated (an invertebrate characteristic).

As in tunicates an *atrial cavity*, a specialized feature probably associated with the animal's particular habits of life, surrounds the pharynx. Water, passing from the gill slits into this atrial cavity, is discharged to the outside through a relatively small *atriopore* located about two-thirds of the way back on the ventral side of the body. Thus the delicate respiratory membranes are removed from the surface of the body where they would be seriously damaged, if not destroyed, as the animal pushes its way through the sand.

Growing out ventrally from the intestine is a blind sac, the *liver diverticulum*, lined with glandular epithelium and supplied with a network of blood vessels that represents the beginnings of a vertebrate *hepatic portal system*, since the blood from the food tube has to pass through this capillary strainer in the liver diverticulum before going forward to the gills and thence over the body.

There is no heart present, but a pulsating ventral blood vessel, lying below the pharynx, is larger than the other blood vessels and is prophetic of the future ventral heart of vertebrates.

The gonads are segmental and can be seen from the outside through the transparent body wall. The germ cells are discharged directly into the atrial cavity from which they are carried to the outside by the respiratory current. The sexes are separate.

Unlike urochordates and hemichordates, cephalochordates probably

represent simple advancing forms, and not ones whose simplicity is the result of degradation.

B. SUBPHYLUM VERTEBRATA (CRANIATA)

All vertebrates exhibit at least traces of a backbone, or *vertebral column*, which begins its development around the embryonic notochord and nerve cord. They also have a *distinct head*, including a brain, olfactory organs, eyes, internal ears, and a skull (*cranium*) associated both with these structures and with the anterior portion of the digestive tract. In contrast with the situation in amphioxus, the notochord of vertebrates extends forward only as far as the level of the mid-brain. The pumping organ of the circulatory system is a *ventrally located heart divided into several chambers*, at least one of which is highly muscular.

A parapod of Nereis, a leg of a lobster, or any other invertebrate appendage arises from a single segment. Vertebrate *appendages*, however, are *formed from several segments*, sometimes many. The arm of man receives muscles and nerves from seven different segments. Some of the fishes (notably the skates and rays) have anterior paired fins arising from a score or more of segments. Many invertebrates have a pair of appendages on almost every segment of the body, while others have only a few pairs, for example, four in spiders and three in insects. Vertebrates alone are limited to two pairs. This is a reasonable and logical arrangement because four legs furnish the most efficient and economical support for any sort of an elongated bilaterally symmetrical object, such as a table-top, a bedstead, or a horse. Certain Devonian sharks are an exception to this rule of *never more than two pairs of paired appendages*. Some vertebrates, it is true, have lost one or the other of their pairs of appendages. Snakes, for example, have lost both pairs.

1. Class CYCLOSTOMATA

The lamprey eels and the hagfishes show a great advance in the chordate series over the forms thus far considered, but are so different from other fishes that they have been placed in a class by themselves (Fig. 16). They are called "cyclostomes" (*cyclo*, round; *stoma*, mouth) for the reason that, instead of typical vertebrate jaws, they have round jawless sucker-like mouths by which they attach themselves to the sides of fishes or to other objects. They are more committed to a life of parasitism than any other vertebrate, and when one fastens to a fish, it may rasp a hole with its filelike horny teeth that are attached to its muscular "tongue," quite through the skin of the unfortunate host whose death eventually results.

Cyclostomes are distinguished chiefly by the absence of certain customary

fishlike structures. They are not only jawless, but are also without paired fins, scales, swim bladder, cloaca, oviducts, true mesodermal teeth, vertebral centra, ribs, or bones of any kind. They have only one external nasal opening instead of the pair present in most vertebrates. They breathe by means of internal gills. All are eel-like in shape, but are not to be confused with true eels, which have a bony skeleton including jaws, instead of a skeleton consisting principally of a persistent notochord.

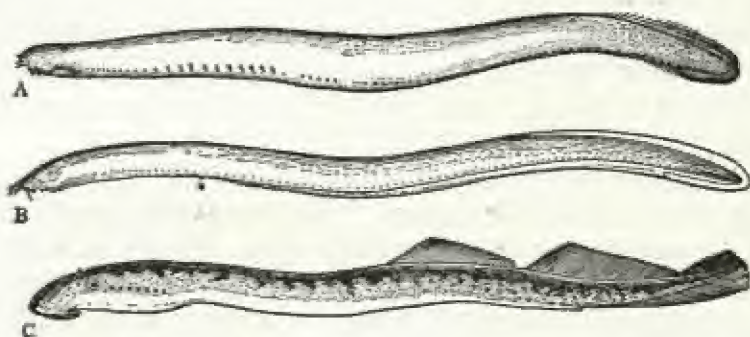


Fig. 16. CYCLOSTOMES. A, *Bdellostoma*. Light apertures along entire length are mucous pits; larger, dark apertures are branchial openings. B, *Myxine*. Left common branchial aperture is at *. C, *Petromyzon*. (From Hegner, *College Zoology*, copyright 1942, and Dean, *Fishes Living and Fossil*, copyright 1895, by permission of The Macmillan Company, publishers of both books.)

The larval lamprey is so different from the adult that it was formerly assigned to a distinct genus and named *Ammocoetes* before its whole life history was known. In its early stages an endostyle-like groove is present in the pharynx. Later this groove pinches off and gives rise to a subpharyngeal gland believed by some to be homologous with the thyroid gland of other vertebrates.

Cyclostomes are usually marine in habitat although they frequent fresh waters to breed, and some species are permanent fresh-water inhabitants.

Lampreys scoop out a nest in the sandy bottom of a flowing stream in which to deposit their eggs, meanwhile fastening themselves by means of their sucktorial mouths to a stone in order not to be carried down stream. This habit has given rise to their genus name of *Petromyzon* (*petros*, rock; *myzon*, sucker).

Hagfishes are particularly slippery creatures, often producing so much mucus when uncomfortably confined in a bucket of stagnant water that the water is thickened into a gluey mass. Linnaeus describes *Myxine glutinosa*, a

European hagfish, in compact Latin: "*Intrat et devorat pisces; aquam in gluten mutat.*"

Lampreys have for a long time been used for food, particularly in Europe. Cicero in one of his orations bewailed the tendency of young spend-thrift Romans of his day, who as in every generation were regarded by their elders as going to the dogs, because they spent their time reveling at night and "feasting upon such delicacies as lampreys."

Only a few genera are reported as belonging to North America. The best known American and European genera are: the hagfishes *Myxine* (Atlantic) and *Bdellostoma* (Pacific); the lampreys *Petromyzon*, found in both salt and fresh water, *Ichthyomyzon*, of the Great Lakes and Mississippi Valley; and the brook lamprey, *Lampetra*.

Closely related to the Cyclostomes are the small jawless armored fishes (Fig. 17) known collectively as the *Ostracoderms* (*ostraco*, shell; *derm*, skin). Because of the absence of jaws these two groups are sometimes classified together as the *Agnatha* (*a*, without; *gnath*, jaw). In the ostracoderms, long since extinct inhabitants of fresh waters, thick bony plates developed in the connective tissue membranes of the skin. These plates were large and immovably joined to one another in the head region to form a shell-like structure over this part of the fish. On the rest of the body the scales were smaller, thus permitting the freedom of movement necessary for locomotion.

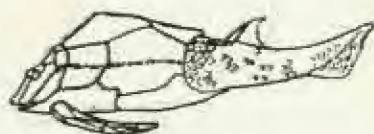


Fig. 17. A restoration of an armored ostracoderm *Pterichthys*, from the Devonian in Scotland. (After Traquair.)

2. Class PISCES

When Pliny (23-79 A.D.) wrote his *Historia Naturalis*, he enumerated 94 kinds of fishes then known to the Roman world. In 1735 Linnaeus listed 478. Today it is estimated that at least 25,000 species are known.

The importance of this class of vertebrates is brought out by the fact that the waters of the earth, of which fishes are the dominant inhabitants, occupy four times the area of the land masses combined. Although primeval fishes lived in fresh water before the oceans became salty, only approximately one species out of twelve now lives in inland fresh waters, while ten are distributed in open oceans or coastal regions and one is a dweller in the darkness of the deep sea.

Fishes vary enormously in size all the way from the dainty *Mistichthys luzonensis* of the Philippines, which is about half an inch long when full grown, to the colossal shark, *Rhinodon typicum* that, according to Haempel,

has been known to attain a length of 65 feet. There is likewise a remarkable range in the body form of fishes, as indicated by representatives shown in outline in Fig. 18.

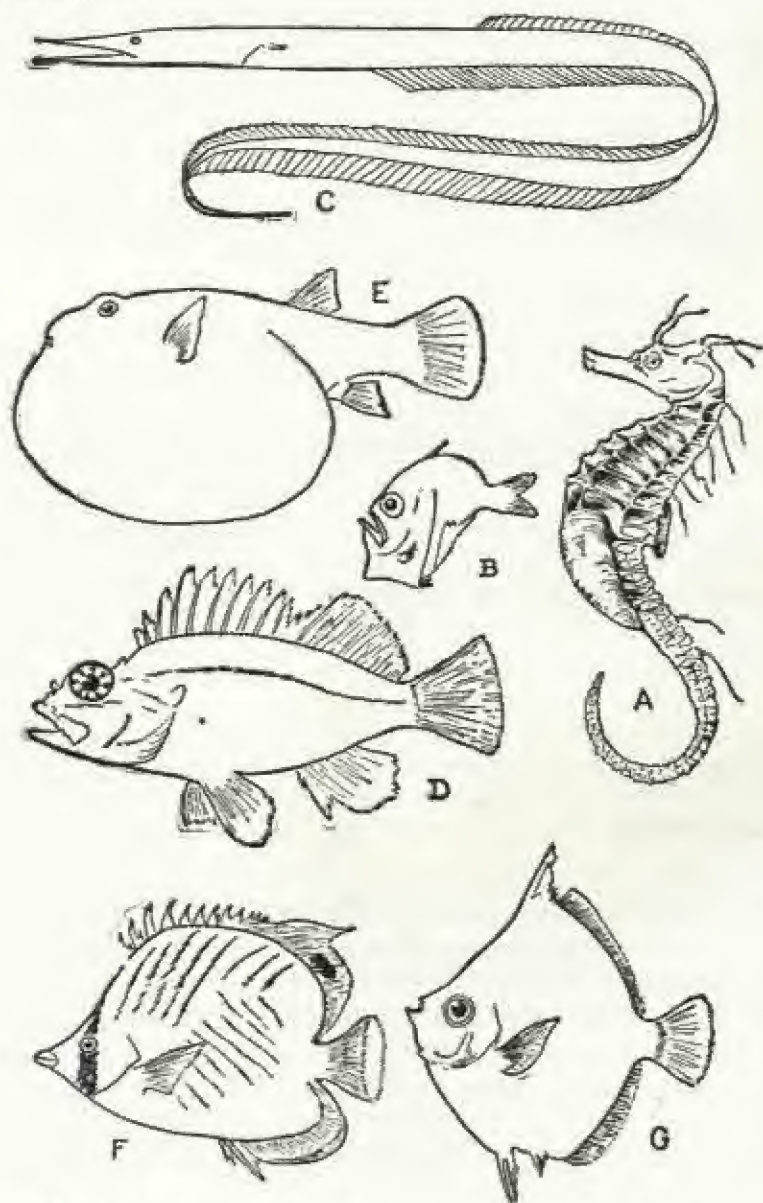


Fig. 18. Some unusual styles of fishes. A, *Hippocampus*; B, *Sternopygus*; C, *Serriuomer*; D, *Sebastopristis*; E, *Tetraodon*; F, *Chaetodon*; G, *Antigonia*. (A, after Hilzheimer; B and C, after Goode and Bean; D to G, Hawaiian fishes.)

The key for understanding the fish plan is to be sought in the adaptation of these animals to life in water. For example, their chief respiratory organs are internal gills. The tail, which frequently is more extensive than all the rest of the body, is the main organ of propulsion, entirely effective in sculling through the resistant medium of water, but quite useless in thin air. The other unpaired fins as well as the paired ones, which are homologous with our arms and legs, are used for steering and to prevent rotation of the body on its long axis, which would otherwise occur as the result of the sweeping strokes of the tail.

As in all higher vertebrates, skeletal rings, the beginnings of the centra of vertebrae, encircle the embryonic notochord of most fishes. During development, these rings gradually fill in to constrict the enclosed notochord considerably in fishes, and obliterate it almost completely in higher forms. Well-developed skulls, consisting of elements associated with both brain and gills, first occur in fishes. In some of the lowest fishes (*Cladoselache*, for example) it can be seen that biting jaws arise as modifications of the most anterior of the gill supports. Because of the presence of jaws, fishes and all higher vertebrates may be grouped together as Gnathostomata (*gnath*, jaw; *stoma*, mouth).

As far as living fishes are concerned, the Pisces may be divided into two subclasses:

- a. CHONDRICHTHYES (*chondro*, cartilage; *ichthy*, fish)
- b. OSTEICHTHYES (*osteo*, bone)

a. Subclass CHONDRICHTHYES

The cartilaginous fishes are so called because their skeletons are entirely of cartilage, the material commonly called gristle. There is considerable evidence that the absence of bone from these animals may be a degenerate condition. Many believe that the ancestors of all the fishes were forms similar to the Ostracoderms.

None of the cartilaginous fishes has an air bladder. The intestinal surface available for both secretion and absorption is considerably increased by a spiral valve (Fig. 212), a tightly coiled fold of the inner part of the intestinal wall.

The Orders of cartilaginous fishes include: (1) CLADOSELACHII; (2) ELASMOBRANCHII; and (3) HOLOCEPHALI.

(1) CLADOSELACHIANS.—The long extinct, primitive sharks belonging to the genus *Cladoselache* possessed many interesting features (Fig. 19). The jaws of these ancient sharks were clearly in line with the gill arches

which lay immediately behind them. In these animals it is even more obvious than in modern sharks that the jaws represent the first pair of gill arches. The ventral halves of the first arches have become the lower jaw while the dorsal halves, tilted forward, have become the upper jaw. A rudimentary vertebral column, consisting of an unconstricted notochord onto which were laced vertebral arches, was present.

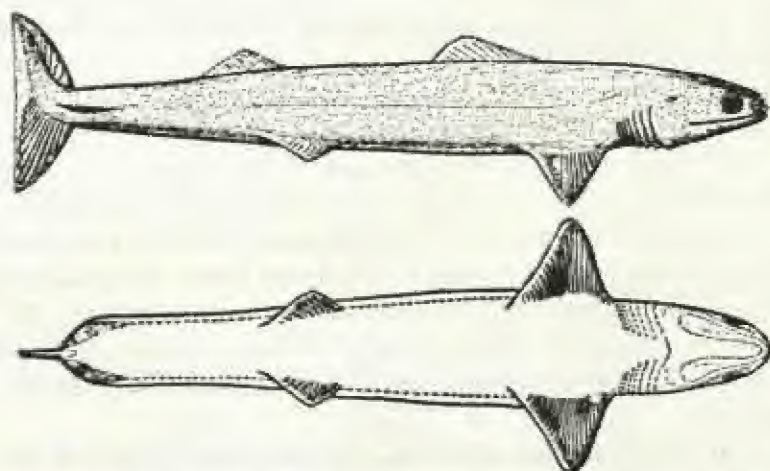


Fig. 19. Restoration of *Cladoselache fylleri*, lateral and ventral views. (From Parker and Haswell, *A Text-Book of Zoology*, copyright 1940, by permission of The Macmillan Company, publishers.)

The fins of *Cladoselache* had broad attachments to the body, a condition which may be cited in support of the fin-fold theory of origin of appendages. According to this theory (Fig. 14) the first appendages were a set of fin folds, including: (1) a continuous median fin extending along the dorsal side of the body, around the tail and forward along the ventral side of the body as far as the anus; (2) a pair of ventro-lateral folds extending from the anal region forward to points immediately behind the last gill openings. Individual fins may have been derived from the dropping out of portions of these folds and the retention of other portions. The primitive individual fins would therefore presumably have broad attachments, such as those of *Cladoselache*. Then a later development would be the narrowing of the base from which the fins fan out, as in many modern fishes.

(2) ELASMOBRANCHIS (gristle fishes).—Most living cartilaginous fishes are elasmobranchs, including the sharks (Suborder *Selachii*) and the skates and rays (Suborder *Batoidea*). The sharks, including dogfishes and their

allies (Fig. 20A and c), all graceful, elongated, streamlined animals, actively prey upon other fishes. The rays, with the skates, torpedoes, guitar fishes, and their allies, on the contrary, are flattened sluggish bottom feeders (Fig. 20B). In the Batoidea the pectoral fins, considerably enlarged, are the organs of propulsion.

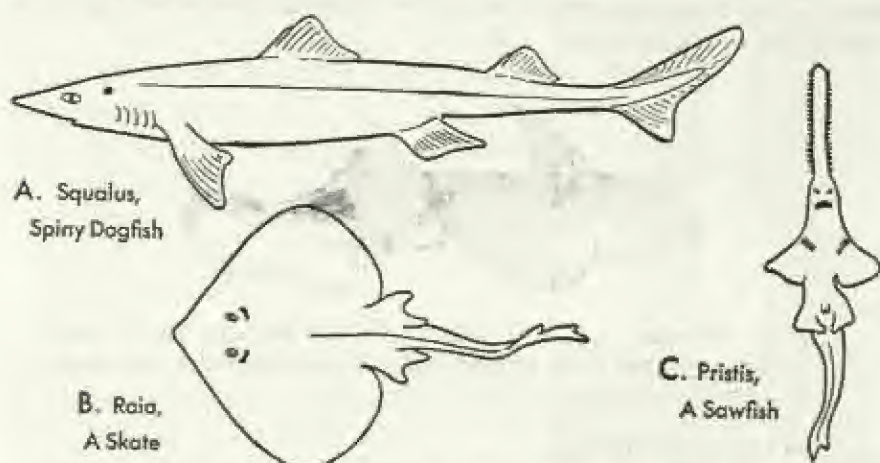


Fig. 20. ELASMOBRANCHS. (A, after Dean; B, after Goode and Bean; C, after Boas.)

An elasmobranch may be distinguished by the following characteristics: (1) a large mouth ventral in position rather than terminal; (2) separate openings of the gill slits (usually five pairs) not concealed as in other fishes behind a gill cover; (3) dorso-ventrally flattened head; (4) *placoid scales*, resembling tiny thumb tacks embedded, point up, in the skin without shingling over each other like ordinary fish scales; (5) tail *heterocercal*, that is, with the vertebral column extending into the dorsal part of the caudal fin; (6) paired pelvic fins modified into "clasp ing organs" in the male, permitting internal fertilization of the egg; and (7) the production of a relatively small number of eggs that in some species are covered with shells and then laid, while in others they develop into some size within the oviduct of the female before the young are born alive.

(3) HOLOCEPHALIANS.—Biological interest in the uncommon and bizarre "elephant fishes," or "spook fishes," centers in their intermediate anatomical position between elasmobranchs and other fishes. They differ from elasmobranchs in a number of respects among which are: (1) small size of mouth; (2) scarcity of scales; and (3) presence of a gill cover, or *operculum*, a fold of the body wall extending over the gill slits but with a free posterior margin under which the respiratory current leaves the body.

The name holocephali (*holos*, whole; *cephalon*, head) is given to them because the upper jaw is immovably fused with the cranium after the manner of higher forms, instead of being indirectly suspended by means of ligaments and cartilages as in elasmobranchs.

Of the three living genera, *Chimaera* (Fig. 21) is found on the Pacific coast of North America, as well as on the coasts of Europe and Japan and at the Cape of Good Hope.

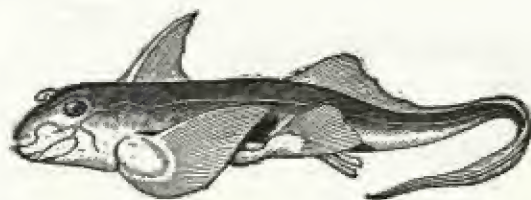


Fig. 21. *Chimaera*, a holocephalian fish. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Bridge.)

b. Subclass OSTEICHTHYES

The modern bony fishes are grouped into the subclass Osteichthyes. At least a part of the skeleton is ossified. Over the skull and pectoral girdle region, investing bony plates are laid down in the dermal portion of the skin. The gills are protected by an opercular fold which has investing bony supports. No claspers are present. Air bladders, outgrowths from the pharynx, are present in all bony fish except a few teleosts.

There are three orders of bony fishes: (1) CROSSOPTERYGII; (2) DIPNOI; and (3) ACTINOPTERYGII.

(1) CROSSOPTERYGIANS.—The Crossopterygii are commonly called lobe-finned fishes because each of their paired fins has a thick, fleshy basal lobe. The skeletal support of this fin consists of a single basal element followed by two bones beyond which are a number of irregular small bones. This condition suggests the plan of the land type of appendage. Other features of this group are: (1) air bladders serving as lungs; (2) a spiral valve in the intestine; and (3) nasal cavities opening into the roof of the mouth cavity. These fish are believed to be the ancestors of land animals.

All members of this group are extinct with the exception of *Latimeria* which is represented by one specimen, about 5 feet long, brought up in a net off the coast of South Africa in 1939. Unfortunately the internal parts of this specimen were destroyed before its zoological significance became known.

(2) DIPNOANS.—As the word dipnoi (*di*, two; *pneum*, air) suggests, the “lungfishes” have two ways of breathing, that is, by means of gills and by a modified swim bladder, or lung (Fig. 330).

They are semitropical, freshwater, primitive fishes dwelling only in countries where wet and dry seasons alternate, instead of winter and summer. During the dry season the African and South American species bury themselves in muddy pits (Fig. 22) and breathe air like land animals, but when the rainy season supplies an abundance of water they swim about fish-fashion, breathing through gills. This passive method of bridging over a season of unfavorable dryness is termed *aestivation*, corresponding to *hibernation*, or the habit of animals like bears, bats, and woodchucks, which retire from activity during the cold winter season.

Other interesting features of these fishes are: (1) a spiral valve; (2) nasal passages opening into the roof of the mouth cavity; and (3) fleshy portions in the paired fins.

There are no lungfishes in North America, and only three living genera are known anywhere. These are *Protopterus* in Africa; *Neoceratodus* in Australia (Fig. 23); and *Lepidosiren* in Brazil (Fig. 24). They possess

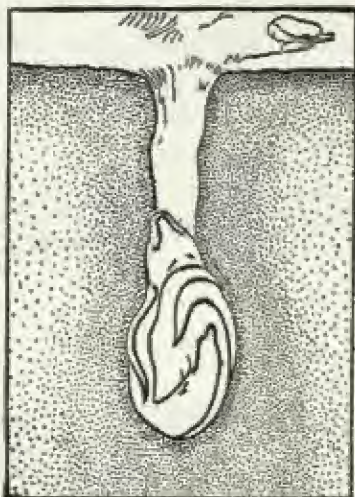


Fig. 22. The African lungfish, *Protopterus*, undergoing aestivation in the mud during the dry season. (After Hiltzheimer.)



Fig. 23. Australian lungfish, *Neoceratodus*. (After Bridge.)

much interest for the zoölogist not only by reason of their peculiar habits and rarity, but also because of the intermediate combination of their anatomical characters which puts them in a class by themselves.

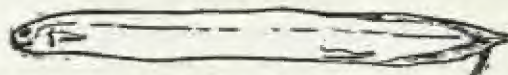


Fig. 24. Brazilian lungfish, *Lepidosiren*. (After Lankester.)

(3) ACTINOPTERYGIANS.—Included among the ray-finned fishes (*actin*, ray; *pteryg*, fin) are the several groups possessing fins with no basal lobes

but with their entire free parts membranous and supported by slender dermal rays. Their nasal pits do not communicate with the mouth cavity. This group includes 3 sub-orders: *Chondrostei*, *Holostei* and *Teleostei*.

(a) **Chondrostceans.**—Those ray-finned fishes which have superficial, dermal, bony plates but an inner skeleton composed essentially of cartilage are called *Chondrostei* (*chondro*, cartilage; *osteo*, bone). These animals also possess a spiral valve and ganoid scales. Among the living members of this group are *Polypterus*, *Acipenser*, *Scaphirhynchus*, and *Polyodon* (Fig. 25).

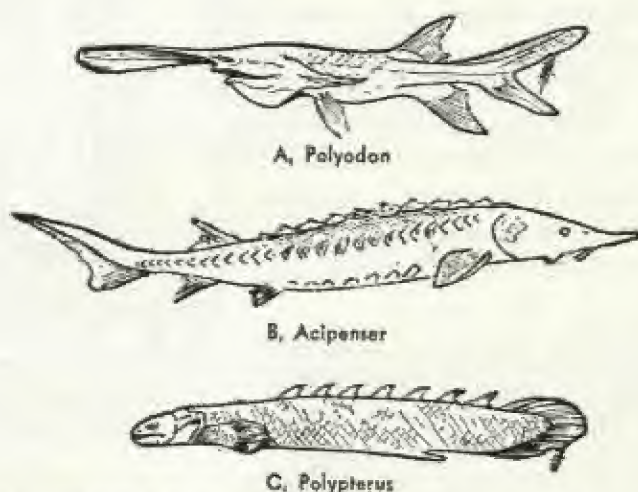


Fig. 25. CHONDROSTEI. A, *Polyodon*; B, *Acipenser*; C, *Polypterus*. (A, after Boas; B and C after Bridge.)

Polypterus (*poly*, many; *pter*, fin), so named because it has a row of small dorsal fins, is found in the tropical fresh waters of Africa. A well-developed pair of swim bladders is connected with the ventral side of the pharynx. A secondarily acquired basal lobe in the pectoral fins has led some taxonomists to include this animal among the Crossopterygii.

Acipenser and *Scaphirhynchus* are the sturgeons of the rivers and lakes of the Northern Hemisphere. Caviar, the delicacy made famous by the Russians, is the eggs of sturgeons. Like the sharks these animals have a rostrum, a ventral mouth, and a heterocercal tail. The scales are reduced in number. In *Polyodon*, the Mississippi spoon-bill, the rostrum is greatly enlarged into a dorso-ventrally flattened, paddle-like structure and the skin is almost devoid of scales. The sturgeons and spoon-bills have a persistent, unconstricted notochord onto which cartilaginous arches are laced by connective tissue.

(b) **Holosteans.**—Those ray-finned fishes which have superficial, dermal, bony plates and also a rather completely ossified inner replacing skeleton are called *Holostei* (*holo*, complete; *osteo*, bone). Other features are: (1) a reduced spiral valve; (2) bony vertebrae; and (3) ganoid scales. There are only two living genera of this group. *Lepidosteus* (Fig. 26A), the garpike of the fresh waters of North America, possesses heavy, shiny, ganoid scales which fit together edge to edge, rarely overlapping, like the tiles around a fireplace. *Amia* (Fig. 26B), the freshwater dogfish of the United States, has overlapping, cycloid scales on the trunk and tail regions, ganoid scales being limited to the head region.

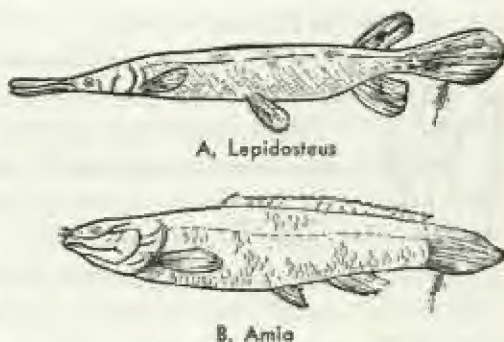


Fig. 26. HOLOSTEI. A, *Lepidosteus*; B, *Amia*. (A, after Goode; B, after Bridge.)

The Chondrostei and Holostei are frequently referred to as the Ganoid fishes, with the former being called the cartilaginous ganoids and the latter, the bony ganoids.

(c) **Teleosts.**—The *Teleostei* (*tele*, entire; *osteo*, bone) are the true bony fishes. They constitute probably 90 per cent of all known kinds of fishes. They have an almost completely bony skeleton; no spiral valve; thin, round overlapping scales on most species; and a homocercal tail. A few unusual representatives out of the great variety of teleosts are suggested by outline sketches in Figure 18. Some of the best known teleosts are herring, salmon, trout, eels, catfish, mackerel, carps, pickerel, perch, flounders, and cod. Of the carps alone there are approximately 1000 species.

3. Class AMPHIBIA

The clumsy amphibians (*amphi*, both; *bios*, life), like Dr. Jekyll and Mr. Hyde, typically lead a double life, that is, first in the water and then on the land. As a class they bridge one of the greatest gaps in vertebrate evolution. The result of this ambitious attempt is that they present a medley of makeshift adaptations, which, while leaving them still a long way from vertebrate perfection, nevertheless make them of particular interest to the student of comparative biology.

Along with access to two different habitats they must encounter a double set of enemies, but at the same time they have two avenues of escape, land and water.

The earliest record of any walking vertebrate is a single illuminating footprint, as unique as that which Robinson Crusoe found in the sand of his island beach, left in the Upper Devonian shales of Pennsylvania, and now to be seen in the Peabody Museum of Yale University. The three-toed fossil ancestor of the amphibians that made this famous footprint has been christened *Thinopus* (Fig. 27).



Fig. 27. *Thinopus*, the oldest known footprint.

(After Thom.)

Among the dual adjustments that any animal living a part of the time submerged in water and a part of the time upon land must make, are those associated with *locomotion* and *protection against desiccation*.

In water an elongated fishlike body, propelled by a muscular tail, has proved to be the most efficient mechanism for locomotion. On land such an arrangement would be out of the question, because in thin air a propeller that could develop power enough to move the body at all would necessitate so great an addition of heavy muscles as to defeat the possibility of aerial or terrestrial locomotion. When the weight of the body is no longer supported by a surrounding medium of water, the two pairs of appendages become modified into legs which act as levers to lift the body away from frictional contact with the ground. It is quite possible to equip such levers with adequate muscles without adding excessively to the entire weight to be moved.

Amphibians, like all land animals, are therefore tetrapods (*tetra*, four; *pod*, foot). At best, however, they are not particularly successful at locomotion on land.

The legs of salamanders, ridiculously small and inadequate, cannot even lift the body from the ground, for instead of being directed ventrally as supports, they project laterally, and can be used only slightly in poking the wriggling body along over the ground. Even in frogs and toads, where amphibian legs reach their highest development, such locomotor appendages are so inefficiently anchored to a single vertebra of the supporting backbone that these animals cannot bear their weight upon them in the sustained manner necessary for standing or walking, and can progress only by the momentary exertion of hopping or jumping. When not locomoting they never stand but always sit.

The problem of protection against desiccation arises from the fact that the air, usually far from saturated with moisture, takes up water rapidly from any moist surface. The cells of the body, as complex chemical laboratories, must contain considerable water to permit metabolic processes to go on. One phase of this problem is that of *breathing*.

The essential feature of every breathing device is a delicate wall, or membrane, separating blood from the oxygen-containing medium. In submerged animals, *gills*, thin-walled structures containing blood and hanging in water in which oxygen is dissolved, fulfil this condition. When exposed for any considerable time to free air, however, thin-walled gills dry up and collapse, making gaseous exchange no longer possible. In animals breathing air, *lungs* are developed. These are enclosed sacs in which an enormous expanse of capillary blood vessels, behind very thin moist walls, is exposed to air. The drying up of this kind of wall is prevented because openings from the lungs to the outside through which evaporation can occur are relatively small, and also the air on the way to the lungs may be moistened in the respiratory passages.

Amphibians not only utilize gills and primitive lungs in respiration but they also exchange gases to a very large extent *directly through the skin*, which, so long as it is kept moist, may remain thin enough to serve as the membrane separating the blood from the surrounding air. Consequently these animals can live only in moist places. On the other hand, higher land animals, in which an efficient pulmonary system is formed, are not restricted, because they develop a thick, relatively dry integument which is resistant to desiccation. Relatively inefficient respiratory organs, together with various other anatomical handicaps, prevent amphibians from maintaining a body temperature independent of that of their surroundings. Since they can never be active when it is cold, they are excluded entirely from frigid regions, while in temperate zones, where winter condemns them to hibernation, they are able to exercise seasonal activity for only a part of the time.

The problem of desiccation is also involved in the breeding habits of amphibians because they have not made the changes required of true land animals. In the case of reptiles, birds, and mammals, the embryo very early becomes enclosed in an amnion (Fig. 34), a liquid-filled sac produced by the embryo itself. As this amnion persists until hatching or birth, the embryo is protected in liquid throughout its development. No amnion is produced by embryos of lower vertebrates including the Amphibia. The latter must, therefore, go back to the water to breed in most cases. A few avoid this requirement by various means (Fig. 28). Some tree frogs lay their eggs in rain-filled holes in trees or pouches formed by folding leaves. Others carry their eggs about in various ways in pouches or pits on the body. A few lay their eggs in very moist places, beneath logs or stones.

Furthermore, the *metamorphosis* of such an amphibian as a frog or a toad, necessitated by its emergence from water to land, works profound changes both in its structure and in its feeding habits. During its lifetime the



Fig. 28. Care of young among Amphibia. a, nests of *Hyla faber* built of mud. (After Wiedersheim.) b, *Rhacophorus schlegelii* of Japan in amplexation within a hole in a muddy bank of a stream. The eggs are deposited in a mass of foamy mucus, and washed out into the stream below by the rain. (After Wiedersheim.) c, a Gymnophiona, *Ichthyophis glutinosus*, guarding its eggs. (After P. & F. Sarasin.) d, the "nurse frog" of Europe, *Alytes obstetricans*. The male carries strings of eggs attached to its hind legs. (After Cope.) e, *Hyla goeldii*, with eggs glued to back of female. (After Ihring.) f, *Nototrema pygmaeum*, female with dorsal brood pouch containing only a few large eggs. (After Brandes and Schoenichen.) g, South American toad, *Pipa dorsigera*, the eggs of which are deposited in pits upon the spongy back of the female by means of the everted cloaca, that serves as ovipositor. They remain in the back until the metamorphosis of the tadpoles into tiny toads. (After Bartlett.) h, *Rhinoderma darwini*, section of head region showing eggs carried within the vocal sac, the position of which when inflated is represented by the dotted circle. (After Wiedersheim.) i, *Arthroleptis reychellensis*, the tadpoles of which are transported to fresh pools by being attached to the back of the male. (After Brauer.)

toad changes its diet six times. While in the egg it absorbs the *yolk* stored within; then, upon hatching, it develops a temporary mouth and eats its way out through the *jelly* of the egg envelopes; next it becomes a free tadpole, swimming about by means of a fishlike tail, and feeding mainly upon *vegetation* found in the water. With the growing pains of its coming transformation it loses its temporary mouth and along with it the appetite for vegetable food: Tiny legs and arms now sprout out through slits in the skin,

and instead of swimming about much the little toad sits quietly in its shirt-sleeves and devotes itself introspectively to the task of making its *tail substance* over into more useful parts of the body. By this time cold weather is approaching and it goes into a long winter retirement during which its only food is a pair of *fat bodies*, peculiar nutritive storage organs attached near the gonads in the body cavity and provided to meet the intervening demands of hibernation. With the warmth of returning spring the young toad, meanwhile equipped with a new mouth and a marvelous lassoing tongue, emerges into a life of carnivorous activity upon land, catching *slugs* and *insects* for a living.

It is not very difficult to recognize amphibians, although by the uncritical they are sometimes confused with reptiles. It was Brogniart who in 1804 separated the Amphibia from the Reptilia as independent classes, because the former have fingers and toes without claws; a scaleless skin; two occipital condyles on which the skull articulates with the first vertebra; hind legs attached to the vertebral column by a single sacral vertebra; and young which breathe by means of gills. Reptiles, on the contrary, have claws; scaly skin; a single occipital condyle; two sacral vertebrae; and young which never resort to gill-breathing. In common with the reptiles, amphibians exhibit certain features not found in fishes, including: (1) modification of paired appendages into legs; (2) modification of swim-bladder region into lungs; (3) two completely separate auricles in the heart; (4) development of a middle ear cavity with a bone to transmit vibrations from external tympanic membranes to internal ear.

Living amphibians of approximately 2000 species may be disposed of in three orders: GYMNOPIHONA, URODELA, and ANURA. To these should be added the extinct STEGOCEPHALI, or "Labyrinthodonts," including some 200 species so far discovered.

(1) STEGOCEPHALIANS.—The stegocephalians, whose ancestry has been traced by some biologists back to the lobe-finned crossopterygians, bear a resemblance to living amphibians, although they disappeared from the earth before any known representatives of modern amphibians made their appearance. This fact, as pointed out by Jaekel, is embarrassing when one seeks to establish them as the undoubted ancestors of the amphibians of today. The gap separating these similar groups of animals may sometime be filled by the discovery of intermediate fossil forms.

The stegocephals flourished in the swampy Carboniferous Period, along with giant rushes, mosses, and tree ferns, before there were any birds, insects, or flowers, and when the warm steamy sluggish atmosphere was probably

heavily charged with an abundance of carbon dioxide. They have the distinction of being the earliest four-footed air-breathers on the earth, large awkward creatures with an armor of scales on the head (Fig. 29), and with a brain so small that it could have been easily pulled out through the *foramen magnum* at the back of the skull. The reason for the name "stegocephali" (*stegos*, roof; *cephalon*, head) is that the size of the skull by no means indicates the cranial capacity of these stupid beasts, there being a large attic-like space roofed in above the brain-case itself.

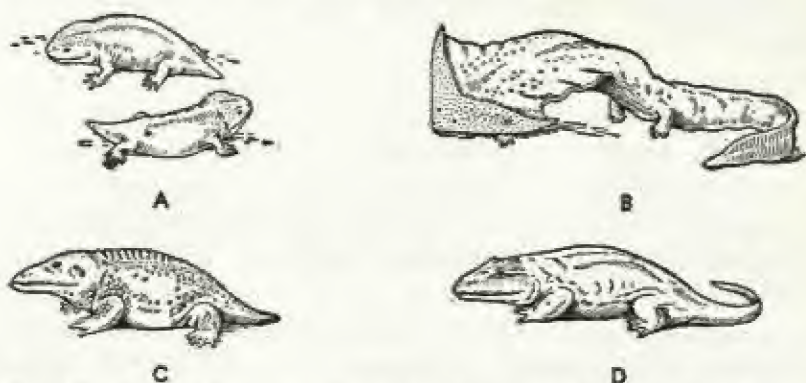


Fig. 29. Stegocephalians, extinct primitive amphibians. A, *Amphibamus*; B, *Diplocaulus*; C, *Cacops*; D, *Eryops*. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Osborn.)

(2) GYMNOPIHONA.—Of modern amphibians the naked, legless Gymnophiona are the least familiar. They include about 50 tropical species from Africa, South America, Ceylon, and India, which burrow in the ground. No fossils are known in this order.



Fig. 30. A tropical wormlike amphibian, *Caecilia*, partly out of its burrow. (After P. & F. Sarasin.)

In appearance these animals resemble worms (Figs. 30 and 28c), although possessing a vertebral column of as many as 250 vertebrae, and numerous other characteristics which place them unmistakably with the Amphibia.

As examples of the order may be cited the "blind caecilian," *Caecilia*, of West Africa, and *Ichthyophis*, of Ceylon.

(3) URODELA (CAUDATA).—Urodeles are newts, mud puppies, and salamanders. They retain their tadpole-like tails throughout life, and many of them never emerge from existence in water, although some do so, living

under stones, rotten logs, and in damp situations generally. Most of them undergo a metamorphosis during which the gills are lost but the tail retained. Some, however, retain their gills and spend their entire lives in the water. *Necturus* (Fig. 31), the mud puppy of the Mississippi River drainage system, is one of these *perennibranchs*, so named because of their persistent

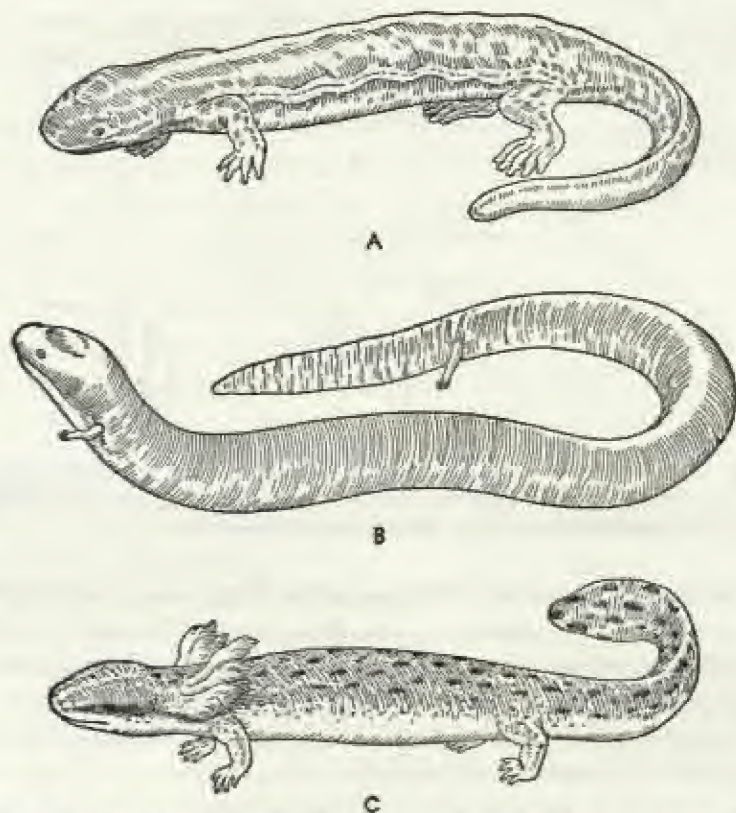


Fig. 31. Urodeles. A, *Cryptobranchus*; B, *Amphiuma*; C, *Necturus*. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Lydekker.)

gills (*perenni*, lasting through the year; *branch*, gill). Other urodeles are: *Amphiuma*, the so-called "Congo Snake" of the Southern United States; *Cryptobranchus*, the "hellbender" of the Ohio River Valley; *Amblystoma*, the commonest American salamander and one which has been extensively used for research in experimental embryology; and *Triton* (Fig. 32), which includes both European and American species.

The "black salamander," *Salamandra atra*, of Switzerland, is particularly adapted to life in the cold tumultuous waters of the high glacial streams

where it lives. Its eggs, only two of which develop at one time, are protected and prevented from being washed away by remaining within the oviduct of the mother, where they hatch and pass through their entire tadpole-hood, reaching a size large enough to insure their safety as independent animals before they are born into the world.

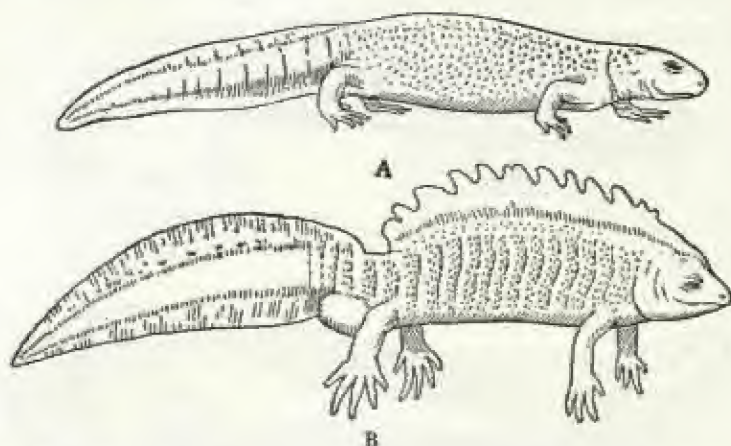


Fig. 32. *Triton cristatus*, a urodele. A, female; B, male in nuptial dress. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Gadow.)

(4) ANURA (SALIENTIA).—Anurans are frogs, toads, and hylas, that lose their tails before becoming adults. They are the first truly vocal vertebrates. Other amphibians as well as fishes, with the exception of those which make sounds by means of their air-bladders, are silent. These quaint and cheerful singers, moreover, are the first animals with a lacrimal gland, and so are enabled to wink and to shed tears. This does not mean that trouble enters the world for the first time with them, since tears and blinking are primary adaptations for keeping the eyes of land animals clean, rather than serving as machinery for the expression of the emotions.

The most populous genus of toads in North America is *Bufo*. There are many genera in other parts of the world, particularly in South America which has a greater variety of amphibians than any other continent.

Some years ago the Department of Agriculture in Washington, in a pamphlet on the economic value of the common toad, *Bufo americanus*, estimated that a single individual in a garden was worth \$19.44 as an insect destroyer. With the changed value of the dollar and the added cost of living, this precise governmental figure should no doubt now be increased. *Scaphiopus* is the American spadefoot toad. *Bombinator* of Europe is a famous

scarlet-bellied toad that escapes attacks of storks because its warning color is associated with a bad taste, as storks have discovered.

The commonest genus of frogs is *Rana*, several species of which are found in Europe and North America. *Xenopus* of Africa, and *Pipa*, of South America, are anurans of particular anatomical interest, as will appear later.

The little tree frogs have adhesive discs at the ends of their fingers and toes that enable them when they leave the water to climb trees where they conceal themselves, persistently sending out their ventriloquistic calls. American genera are: the "cricket frog," *Acris*; the "swamp tree frog," *Pseudacris*; and the common tree frog, *Hyla* (Fig. 33).

Many amphibians are remarkable for the ways in which they care for their eggs and young. Some examples are illustrated by the sketches in Figure 28.



Fig. 33. A tree frog, *Hyla*.
(After Dickerson.)

4. Class REPTILIA

There are about 5500 species of living reptiles, of which over 300 are found in the United States.

Although, as compared with amphibians, their legs lengthen and strengthen, "reptiles" (*repere*, to crawl) are named with an eye to the legless crawling snakes. The group includes not only snakes but also lizards, turtles, and alligators, as well as *Sphenodon*, a New Zealand genus containing a single species. Also included is a vast company of forms now extinct, many of which were gigantic, that dominated the Mesozoic world throughout a dynasty that endured for ages.

Reptiles are the first true land vertebrates freed from the necessity of returning to the water to breed. "Things that before swam in the water now went upon the ground" (Wisdom of Solomon). This saying is true even of alligators, certain turtles, and water snakes which, although they spend much of the time in water, come out upon the land to lay their eggs. Each egg is usually fertilized and then covered with a shell while still inside the body of the female.

As mentioned in the discussion of amphibians, each embryo of a reptile, bird or mammal is surrounded by an *amnion* during most of its development (Fig. 34). The astonishingly rapid growth of any developing embryo necessitates a protective covering for the extremely delicate cells and tissues that

does not involve hampering adaptations for withstanding exposure to dry air or mechanical shocks during their tumultuous multiplication. Growing embryos of fishes and amphibians have such a provision in the surrounding medium of water in which they are immersed, but reptiles and all other conquerors of the land who cannot cradle their growing youngsters in open

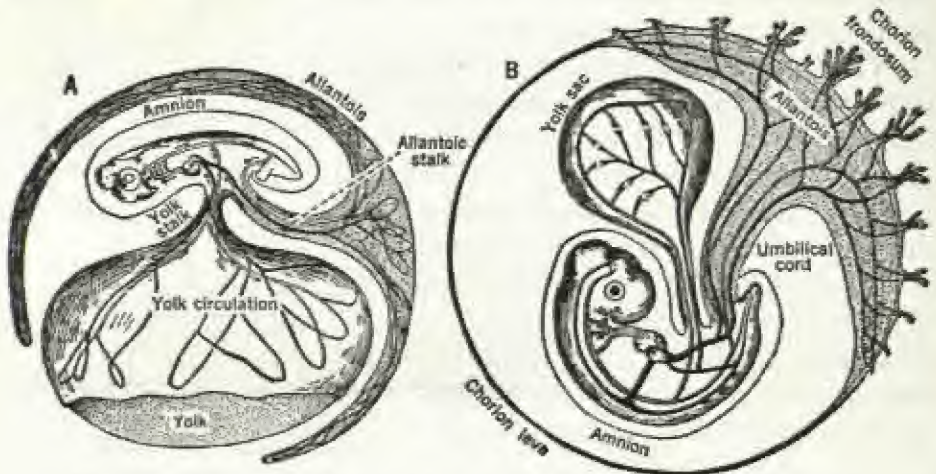


Fig. 34. Diagrams of the embryonic membranes, amnion, allantois, yolk-sac of amniotes, A, Sauropsida (reptiles and birds); B, mammal with primitive allantoic placenta. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Wilder.)

water, depend upon a protective antenatal robe that the young embryo forms about itself. This is the amnion, a thin enveloping sac filled with a secreted watery fluid in which the embryo floats. It may be truly said, therefore, that in a certain sense every vertebrate passes its early life submerged in water. Because all reptiles, birds and mammals have an embryonic amnion, they are collectively known as *Amniota*; while all lower vertebrates in which no amnion develops, are called *Anamnia*.

In the closed amnion sac neither gills nor lungs, nor even body surface, can serve as respiratory organs. Hence, contemporary with the amnion is an *allantois*, an outgrowth from the posterior part of the digestive tract which serves as a temporary breathing and excreting organ. This emergency organ, bearing a rich network of blood vessels, grows out into the space between the amnion and the thin, inner egg-shell membrane, or *chorion*, so that through the latter and the porous egg-shell there is effected the interchange of gases between the blood and the outside world essential to breathing and excretion. In the case of mammals, the egg has no shell, but develops

into a fetus that is parasitically attached to the uterine walls of the mother. The capillary-laden allantois, coming into intimate contact with the richly vascularized wall of the uterus, by interdigitations, forms the *placenta*. It is through this organ that the young animal breathes and excretes until it is born into independence.

Reptiles have a rather thick integument with few glands and many scales. The lungs are usually well developed in adults. The excretory organs (metanephroi) are of a more advanced type than those (mesonephroi) of fishes and amphibians. On the ends of the digits are claws. The skull bears only one occipital condyle for articulation with the first vertebra. In modern species, the pelvic appendages are connected with two sacral vertebrae. A partial or complete partition develops between the right and left sides of the ventricle of the heart. Like the lower vertebrates, however, they are cold-blooded.



Fig. 35. Palaeozoic reptiles. A, *Seymouria*; B, *Labidosaurus*; C, *Cynognathus*, a mammal-like reptile; D, head of *Scymnognathus*, a South-African "dog-toothed" reptile. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Osborn.)

(1) EXTINCT REPTILES.—Extinct reptiles with their fossil remains wrote a long and dramatic chapter in the history of living things upon the earth for modern man to read. Several entire orders, the flying pterosaurs, aquatic ichthyosaurs, and long-necked plesiosaurs, for example, have, so far as is known, left no living descendants, but others have been the ancestors of not only recent reptiles but also birds and mammals.

There are more than a dozen orders of reptiles of which only four include living species. During the Golden Mesozoic Age of Reptiles, which lasted according to some geologists, from 125 to 150 million years, these

ruling animals attained a great diversity of form and adaptation, enabling them to live in a variety of habitats, such as forests, water, swamps, dry land, and air. The imagination is thrilled by a picture of the Mesozoic landscape with its weird reptilian population. Some of these strange creatures of past precamera days are suggested by the sketches in Figure 35.

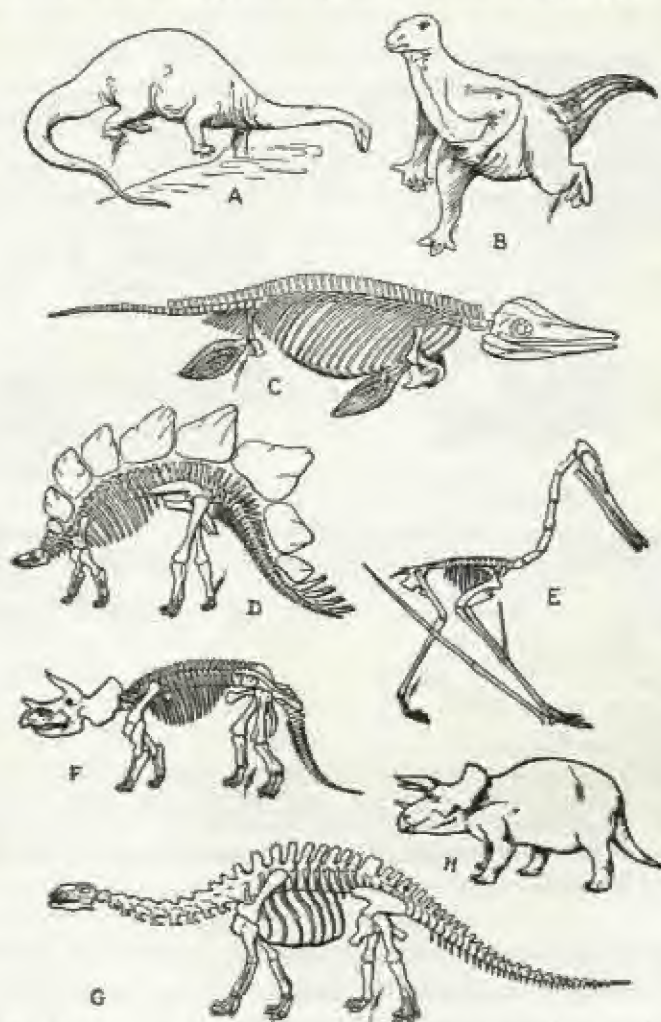


Fig. 36. Various extinct reptiles, selected to indicate diversity of form. They are not drawn to a common scale, but are mostly gigantic in size. A, restoration of *Diplodocus*. (After Smit.) B, restoration of *Iguanodon*. (After Heilmann.) C, *Ichthyosaurus*. (After Conybeare.) D, *Stegosaurus*. (After Marsh.) E, *Pterodactylus*. (After Seeley, but according to Abel in incorrect quadrupedal attitude.) F, *Triceratops* skeleton. (After Marsh.) G, *Brontosaurus*. (After Marsh.) H, restoration of *Triceratops*. (After Nuhn.)

The *cotylosaurs*, or stem-reptiles, were the earliest members of the group (Fig. 35A). Structurally they closely resembled the most primitive of the Amphibia. In external appearance they probably looked like the larger of our lizards.

The *therapsids*, another early group, possessed certain features which indicate they were ancestral to the mammals (Fig. 35). Their teeth were differentiated into the three major types: cutting incisors; large, pointed canines; and grinding molariform teeth. Their jaws also showed a trend toward the mammalian plan.

The *dinosaurs* (Fig. 36B, D, and H), including many species which varied widely in appearance, ranged in size from tiny forms about the size of a hen to the well-known enormous species which were the largest animals ever to walk on the face of the earth. Many of these reptiles were probably bipeds, capable of raising themselves up on their hind legs for more rapid running. To counterbalance the front parts of the body there was a long, rather heavy tail. The front legs, shorter than the hind legs, were presumably used when the animal was resting or walking slowly. These bipedal forms may have been close cousins of the earliest birds, both groups coming from the same immediate ancestral stock. The largest of the dinosaurs were undoubtedly quadrupeds (four-footed). Apparently many of them developed amphibious habits, spending much of their time in lagoons and swamps where the water reduced the weight which it was necessary for their legs to bear.

Of the reptiles which returned to the water to live, the *ichthyosaurs* (*ichthyo*, fish; *saur*, lizard, reptile) were the best adapted to aquatic life (Fig. 36C). Their paired appendages were flippers, modified from typical tetrapod legs. In general appearance they were fish-like. Without doubt they breathed by means of lungs. As amniotes, each of their embryos presumably developed an amnion and an allantois and was incapable of surviving if the egg was laid in the water. A number of specimens have been found with small complete skeletons inside the body of the adult. It is believed, therefore, that these animals were viviparous.

Some of the bipedal early reptiles apparently evolved into flying species (Fig. 37). These were *pterosaurs* (*ptero*, wing). The fourth digit of each front appendage became strong and considerably elongated to support the



Fig. 37. A pterosaur. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Osborn.)

wing, a fold of the skin. Just how much of their activity was true flying and how much was gliding is still problematical.

Modern surviving reptiles may be grouped into the following orders: RHYNCHOCEPHALIA, CHELONIA, SQUAMATA, and CROCODYLIA.

(2) RHYNCHOCEPHALIA.—The rhynchocephals, which include many fossil kinds, are represented today by a single surviving genus, *Sphenodon*, or the "tuatara" of New Zealand (Fig. 1). This is a long-tailed, lizard-like animal usually somewhat less than two feet in length as an adult. In common with the many extinct species of this Order, *Sphenodon* shows many primitive reptilian features. It probably owes its survival to its isolation in an area where it did not have to compete with mammals. Reference has already been made to the median eye of this interesting "old curiosity shop" of ancestral peculiarities, and there will be future occasion to rummage further in this anatomical attic for sidelights of the vertebrate past.

(3) CHELONIA.—The chelonians, or turtles and tortoises, modified "reptiles in a box," are unusual in many respects. Their internal organs, in both shape and arrangement, are adapted to fit into a short, broad box formed by the ventral, relatively flat *plastron* and the dorsal, more or less curved *carapace*. This shell consists of bony plates covered over with large, thin,



Fig. 38. Chelonia. A, *Dermochelys* (*Sphargis*) *coriacea*, leather-back turtle; B, *Chelydra serpentina*, snapping turtle. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Lydekker.)

horny scales. The trunk vertebrae are attached to a row of these plates running down the middle of the carapace. Consequently the only flexible portions of the vertebral column are the neck and tail regions. These two regions, together with the four legs, may be withdrawn beneath the shell into a place of protection. Turtles possess toothless jaws encased in horny beaks.

A few of the genera of turtles are: the "leatherback," *Dermochelys* (Fig. 38); the "loggerhead," *Thalassochelys*, which cruises about in salt

water and may attain a weight of several hundred pounds; the "green turtle," *Chelonia mydas*, also a seagoing animal, prized as food; the "snappers," *Chelydra* (Fig. 38) and *Macrochelys*, the latter of which has a bite powerful enough to amputate a foot; the "box turtle," *Terrapene*, that is able to withdraw its head entirely within its shell and to close the door with a hinged lid; and finally, the small beautifully decorated "painted turtle," *Chrysemys*.

America of all the continents is particularly rich in chelonian inhabitants.



Fig. 39. Wall gecko, *Tarentola mauritanica*, a lacertilian. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers, After Lydekker.)



Fig. 40. An Indian lizard, *Draco*, the "flying dragon." (After Hiltzheimer.)

(4) **SQUAMATA.**—The squamates are reptiles clothed with a great number of regularly placed scales which cannot be separately detached like the scales of bony fishes but are connected together into a continuous armor. They comprise two suborders: the **LACERTILLA**, or lizards, and the **OPHIDIA**, or snakes, distinguished from each other by the fact that the former have movable eyelids, visible carpits and usually legs, while the latter do not.

The lizards are typically sun worshippers, dwelling in regions of much sunshine, and for the most part avoiding water. A notable exception is the water lizard, *Amblyrhynchus*, which is an inhabitant of the rocky shores of the Galapagos Islands.

The "geckos," of the Malay region and the Mediterranean countries, have adhesive toes that enable them to clamber about with great agility after flies and other insects in trees and upon the walls inside of houses (Fig. 39). The "flying dragon" of India, *Draco* (Fig. 40), is able to volplane

from branch to branch of the trees that it inhabits, by means of a capelike expansion of the skin down the sides.

Iguana is a large arboreal Mexican lizard of fierce aspect but harmless habit which is regarded as good to eat. The giant of them all is the rare *Varanus komodoensis*, the "dragon" of the East Indies, which may attain a length of twelve feet.



Fig. 41. An African lizard, *Chameleon*, which has a long extensile tongue and is famous for its power of changing color. (After Hilzheimer.)

The "chameleon," *Chameleon* (Fig. 41), has a prehensile tail and grasping feet and flaunts a Joseph's coat of many colors. It is a native of Africa, although its name is sometimes erroneously applied to the little American *Anolis* (Fig. 42) of changeable colors that inhabits the cane fields of the South and preys upon the insects which are attracted by the sweet juice that oozes from the cane.



Fig. 42. An American "chameleon," *Anolis*. (After Ditmars.)

The "glass snake," *Ophisaurus* of the Old World, and the "slow worm," *Amphisbaena*, are legless lizards.

In the desert region of the southwestern United States are found the grotesque "horned toad," *Phrynosoma* (Fig. 43), that is called a toad only

by the indiscriminating, and the "Gila monster," *Heloderma* (Fig. 44), an ugly black and orange beast, with a large round stubby tail, which is the only lizard whose bite is venomous.

The serpents are the legless snakes, described by Ruskin as "a wave but without wind, a current but with no fall." They walk upon their numerous ribs, or "jerk themselves forward by a rapid straightening of their sinuous curves" (Thomson). The curious arrangement of the internal organs of these creatures has a direct connection with their external architecture.

Most snakes have few human friends, in spite of the fact that most of them are beneficial animals, feeding largely upon injurious insects and small rodents.

They have suffered vicariously from an unsavory reputation ever since one of their number was reported to have taken part in the original eternal triangle play in the Garden of Eden.



Fig. 43. The "horned toad," *Phrynosoma*, of the desert region of southwestern United States. It is not a "toad" but a lizard. (From Hegner, *College Zoology*, copyright 1942, by permission of The Macmillan Company, publishers. After Gadow.)

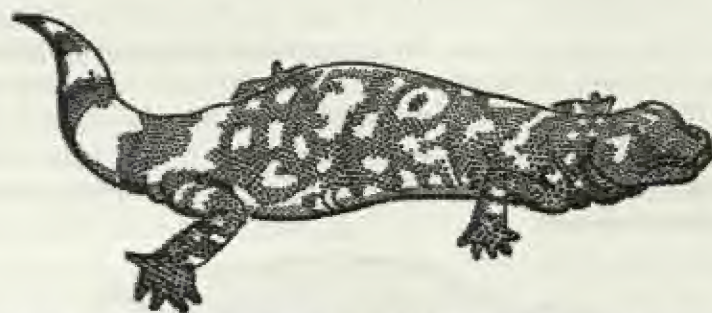


Fig. 44. "Gila monster," *Heloderma*, the only known venomous lizard.

Of approximately 110 species in the United States, less than 20 are venomous. The most dangerous of these, so far as man is concerned, are the several species of rattlesnakes in the genus *Crotalus* (Fig. 45); the "copperhead," *Agkistrodon mokasen*, and the "water moccasin," *Agkistrodon piscivorus*, of the South; and the "coral snakes," *Micrurus*, also of the South.

The "black snake," *Coluber*; the "puff adder," *Heterodon*; the "milk snake," *Lampropeltis*; and the "garter snake," *Thamnophis*, are among the common harmless varieties.

(5) CROCODYLIA.—The crocodiles are, in a number of respects, the most advanced of the reptiles. Their lungs are very efficient organs. Their heart has two completely separate ventricles, a condition found also in birds and mammals. The brain has large cerebral hemispheres. The Crocodilia include

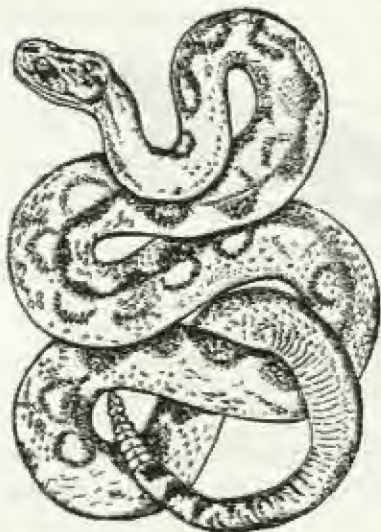


Fig. 45. Texas rattlesnake, *Crotalus*. (After Stejneger.)

the *crocodiles* proper of India, China, Africa, the Malay Archipelago, Central America, Mexico, and the southeastern United States; the broad-snouted *alligators* of the Mississippi Basin, Florida, and China (Fig. 46); the *caimans* of Central and South America; and the narrow-snouted *gavials* of the Ganges in India. All are inhabitants of tropical or semi-tropical countries and, though clumsy and stiff-necked on land, are quite at home in shallow water, where their powerful laterally compressed tails enable them both to swim forward and to strike powerful side blows.

5. Class AVES

All birds, of which there are perhaps 15,000 species, have feathers. This one conspicuous characteristic suffices to identify a bird, even to a child, for no other animals have feathers. The vertebrate type probably reaches its highest differentiation, in certain directions at least, in birds, and for this reason it is not at all difficult to find many other distinguishing characteristics, aside from feathers, in this familiar and much studied class of animals.



Fig. 46. Alligator.

The secret of the anatomical peculiarities of birds lies in their adaptation to flight. Speed of animal locomotion culminates in birds. The same combination of organs which converts a fish into a living submarine and adapts a reptile to a life of continuous contact with the earth, transforms a bird into a flying machine heavier than air.

The skeletal framework of a bird, comparable bone by bone with that of other vertebrates, is compacted together, thus affording the smallest pos-

sible bulk to pass through the air, although the surfaces of individual bones remain relatively expansive for the attachment of greatly developed muscles of flight. The surfaces of the breastbone, the humeral heads, and the sacro-pelvic complex particularly, are increased beyond those of other vertebrates. Every possible part of a bird is transferred from the anatomical suburbs into the compact urban district of the body. The heaviest parts hang beneath the line of support joining the wing-sockets where the power is applied in flight. Considerable weight is shifted from the periphery to the center by means of the replacement of heavy dense teeth, commonly found in the head of other vertebrates, by the light horny beak, while a tough muscular centralized gizzard, containing powerful grinding stones, does the work which teeth once did in ancestral birds.

The cumbersome trailing reptilian tail is telescoped into a degenerate skeletal stub, thus centralizing weight. In place of it a secondary tail of light air-resisting feathers is added as a rudder in flight. The presence in birds of a bony tail, composed of several foreshortened vertebrae instead of a single bone which might better have served as a support for the tail feathers, is one of the numerous evidences of reptilian ancestry. Indeed someone has happily described birds as "glorified reptiles."

The bones of a bird are not only compact but are also lightened and adapted as parts of a flying machine, by being hollowed out to the limit of mechanical safety. Furthermore, bodily weight is particularly counterbalanced by the development of numerous air sacs that grow out from the lungs, occupying all available spaces between the internal organs and extending even to the cavities of the hollow bones. Feathers, which clothe a bird, hold a blanket of enveloping air next to the body, that, since it is warmed by the body and is consequently lighter than the surrounding air, adds somewhat to the bird's buoyancy.

In addition, the large intestine, particularly the rectum where the feces are carried, is very much reduced in length. Since flying animals can ill afford to be weighted down with any excess fecal baggage, birds, having no suitable provision for its storage, promptly get rid of it.

The entire support of a bird's body devolves upon the hind legs alone, leaving the fore legs free to serve as wings. The wing is composed largely of feathers attached to an arm terminating in three reduced and partially fused fingers. As a consequence the forelegs, or arms, which are modified and entirely given over to flight, cannot be used for the capture and manipulation of food. The head, therefore, is necessarily not only periscopic but prehensile, being mounted upon an extremely flexible neck and equipped with a forceps-like beak for picking up food. As a result the remarkably

developed eyes, located on either side of a bird's beak, are much nearer their objective than the eyes of any other vertebrate which reaches for its food.

The excessive activity involved in flight is provided for in birds by a relatively larger heart than other animals possess, as well as by a particularly effective respiratory apparatus, which so increases the warmth of the body as to render it constant, regardless of the surrounding temperature. Birds are active, therefore, the year around, in cold as in warm weather, never

becoming sluggish or obliged to hibernate as "cold-blooded" animals do. Enabled ordinarily to rise above the handicaps of temperature and climate, when occasion demands they resort by migration to distant and more congenial localities.

There are two subclasses of the Aves:

(a) **ARCHAEORNITHES** (*archae*, old, primitive; *ornithos*, bird); (b) **NEORNITHES** (*neo*, new).

a. Subclass ARCHAEORNITHES (Primitive Birds)

On account of their light bones and the rapid disintegration of their bodies after death, birds are not subject to fossilization except under the most favorable conditions, and do not, therefore, present so extensively recorded a story of past achievements as reptiles.

The earliest known trace of bird life is the imprint of a single tail feather, discovered in the Jurassic slate quarries of Bavaria.

This unmistakable fragment dates back to



Fig. 47. The oldest known bird, *Archaeopteryx*, showing teeth, three fingers, feathers, and a lizard-like tail. The Berlin specimen. (After Parker and Haswell.)

the middle of the long Age of Reptiles, long before mammals had arisen to become a power upon the earth. In splitting up the fine-grained lithographic stone of the Solenhofen deposit in Bavaria from which this priceless feather came, there were found also at different times later two entire skeletons, crushed flat and embedded in the slate, of the same kind of birds that doubtless produced this famous tail feather. From these slight but convincing remains, the species of this oldest of all known birds, was named *Archaeopteryx lithographica* (Figs. 47 and 48). It was about as large as a crow, had lizard-like teeth set in sockets in the elongate jaws, a long uncentralized bony tail bearing two oblique rows of feathers, a flat

sternum, three fingers with claws terminating each wing instead of one clawless finger as modern birds have, and feathers. They resembled the small dinosaurs so closely that only the presence of feathers has prevented them from being placed among the reptiles.

b. Subclass NEORNITHES (Modern Birds)

The neornithes include all present-day birds in addition to a number of extinct species which resemble modern birds in most respects. The chalk beds of western Kansas, which were laid down at a much later date than the Bavarian slates of Jurassic times, have yielded the fossil remains of extinct birds *with teeth*, for example, *Ichthyornis*, in form resembling a tern, and *Hesperornis* (Fig. 49), a flightless loon-like water bird, of which over a hundred specimens have been found. Excluding the toothed ancestral birds of Kansas, modern birds may be divided, according to flying ability, into two unequal groups, RATITAE and CARINATAE.



Fig. 48. Restoration of *Archæopteryx*, after Heilmann. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Osborn.)



Fig. 49. A toothed loon-like bird, *Hesperornis*, without a keel on the breastbone. From Kansas chalk beds. (After Marsh.)



Fig. 50. A primitive wingless burrowing bird, *Apteryx*, from New Zealand. (Drawn from a specimen in the collection at Brown University.)



Fig. 51. A giant "moa," *Dinornis*, from a mounted specimen eighteen feet in height in the exhibit of the Government of New Zealand at the Panama-Pacific Exposition.

The ratites, none of which are indigenous to North America, are flightless running birds that have powerful legs and small wings. They include ostriches, cassowaries, emus, rheas, and the curious wingless *Apteryx*, or "kiwi" of New Zealand (Fig. 50), that, in the absence of ability to escape by flight, has survived the perils of a hostile world by burrowing in the ground.

In New Zealand also, a land of special interest to the biologist, have been found abundant fossil remains of *Dinornis*, the largest of all known birds, commonly called the "moa" (Fig. 51), which reached a height of at least 18 feet. It is likely that this species of gigantic ostrich-like bird has become extinct within the memory of man for when the whites first came into contact with the native Maoris of New Zealand they had legends about these birds that had been handed down to them from their fathers.

The carinates are flying birds whose wide breastbone has developed an expansive keel, or *carina*, for the attachment of muscles of flight. Ribs made up entirely of bone hold the breastbone firmly in place.

According to Gadow of the British Museum the carinates comprise thirteen orders as named below. A few more or less familiar examples are given to represent each order.

1. COLYMBIFORMES: loons, grebes.
2. SPHENISCIFORMES: penguins.
3. PROCELLARIIFORMES: petrels, albatrosses.
4. CICONIIFORMES: pelicans, herons, cormorants, flamingos, storks.
5. ANSERIFORMES: geese, ducks, swans.
6. FALCONIFORMES: vultures, hawks, eagles, condors.

7. TINAMIFORMES: tinamous.
8. GALLIFORMES: turkeys, fowls, quail.
9. GRUIFORMES: rails, and other marsh birds.
10. CHARADRIIFORMES: plover, sandpipers, and other shore birds, gulls, terns, auks, pigeons, doves.
11. CUCULIFORMES: cuckoos, parrots.
12. CORACIIFORMES: kingfishers, owls, whip-poor-wills, swifts, humming birds, woodpeckers.
13. PASSERIFORMES: flycatchers, sparrows, swallows, vireos, wrens, nuthatches, kinglets, thrushes.

6. Class MAMMALIA

Mammals (*mamma*, breast), of which there are about 15,000 species, are perhaps less spectacular anatomically than reptiles or birds, but in spite of this fact they have come to occupy a dominant place among the vertebrates. Mammals emphasize a new note of coöperation not discoverable to any great extent in the universal competition that elsewhere characterizes creation.

The first mammals to appear on the earth were small and insignificant contemporaries of the gigantic reptiles of the Mesozoic Age. As long as huge carnivorous dinosaurs held sway, the small ancestral mammals, which were probably largely arboreal in habit, kept out of the way and bided their time. Perhaps they hastened that time somewhat by feeding upon the eggs of their terrifying enemies while eluding capture themselves. At any rate it is certain that in the long struggle for a "place in the sun," it has been wits rather than brute force that has enabled mammals to out-distance competitors.

No doubt the mechanism which insures "warm-bloodedness," that is, a constant bodily temperature independent of changes in the surrounding atmosphere, has much to do with the conquest of the earth by mammals. By reason of this important characteristic they have been able to establish themselves not only throughout temperate areas but even in dry deserts and frigid polar regions.

While the highly specialized birds have sacrificed everything to developing the power of locomotion by flight in air, mammals have chosen the better part of improvement along the line of the nervous system, especially in the considerable enlargement of the very important cerebral hemispheres. Achievement in this direction has undoubtedly been the greatest of all factors in determining the present supremacy of the mammalian type. An unusual amount of plasticity and versatility is exhibited among mammals. For example, they vary in size from a field mouse scarcely more than an

inch in length, to whales which may attain a length of over 100 feet, or well over 1000 inches.

Mammals are variously fitted for successful life in such diverse habitats as on the land (deer); in water (otters); in burrows (gophers); underground (moles); in open oceans (whales); in forests (monkeys); and in the air (bats).

The most important characteristics of mammals are:

- (1) *Milk Glands*, providing food for the more or less helpless young for some time after birth. Masses of milk glands (breasts) have given us the name Mammalia.
- (2) *Hair*, almost as typical of mammals as feathers are of birds. Occurs at least in embryonic life.
- (3) *Sweat Glands*. One interpretation is that certain sweat glands became modified into milk glands.
- (4) *Enucleate Erythrocytes*. The red blood cells are without nuclei when freed into the blood stream. Nuclei, present as the individual cells form, are extruded from them while they are still in the blood-forming tissues.
- (5) *Seven Cervical (Neck) Vertebrae*, in all except a few species.
- (6) *Muscular Diaphragm*, separating the thoracic cavity, containing lungs and heart, from abdominal cavity.
- (7) *Differentiation of the Teeth* into three major types (cutting incisors, piercing canines, and grinding molars and premolars), a condition foreshadowed in the therapsids, the early reptiles from which mammals arose.

Additional characteristics will be considered during the discussions of the various organ systems.

Living mammals may be arranged in seventeen orders, which fall into three subclasses: PROTOTHERIA, METATHERIA, and EUTHERIA.

a. Subclass PROTOTHERIA

Order Monotremata.—The prototheria (*proto*, first; *ther*, beast) comprise a single order, MONOTREMATA, of which only three genera are living today, namely, *Echidna*, *Proechidna*, and *Ornithorhynchus*. The digestive, urinary, and genital systems empty into a cloaca through which all of them communicate with the outside by a single opening (*mono*, one; *trema*, opening).

Monotremes are curious exceptional mammals that lay relatively large yolk-laden eggs, from which the young are hatched instead of being born

alive in ordinary mammalian fashion. *Ornithorhynchus* incubates its leathery-shelled eggs in a shallow nest of grasses, while *Echidna* forms a temporary pouch from a fold of the skin upon its belly. In this portable nest the newly-laid egg is placed and incubated until hatched and the helpless offspring kept through the precarious days of its early growth and development. The young *Echidna* is fed upon a nutritious substitute for true milk, secreted by the mother from modified sweat glands, which it licks up with its long tongue from tufts of hair on the belly of the mother. No nipples are present and if they were the baby monotreme would not be able to suck, since its lips are prolonged into a horny toothless beak, not at all fitted for the muscular operation of sucking, but useful later for poking into ant-hills after food.



Fig. 52. The "duckbill," *Ornithorhynchus*, an Australian monotreme with webbed toes and a ducklike bill. (After Beddard.)



Fig. 53. The spiny anteater, *Echidna*, a monotreme. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Vogt and Specht.)

In *Ornithorhynchus* (Fig. 52) the beak is large and flattened, giving rise to the name of "duckbill" for this creature, a name all the more appropriate because it lives much of the time in water and has feet with webbed toes like those of a duck. The "incredible duckbill" is a native of South Australia and Tasmania.

Echidna, the spiny anteater (Fig. 53), is found in Australia, Tasmania, and New Guinea.

Proechidna, distinguished from *Echidna* by an unusually long snout that gives it a "ridiculous resemblance to a miniature elephant," is confined to New Guinea.

b. Subclass METATHERIA

Order Marsupialia.—The metatheria (*meta*, after; *ther*, beast), comprising the single order MARSUPIALIA, are primitive, or possibly degenerate, mammals whose young, born prematurely in an extremely helpless condition, are fed upon true milk and carried about in a permanent brood pouch, or *marsupium*.

At first the young vestpocketed marsupials are unable to exercise the necessary muscular effort involved in sucking, and are securely attached in a passive way to the nipple by means of a sphincter-like mouth (Fig. 54),



Fig. 54. A young marsupial, *Smynthopsis*, with its snout gripped by the cup-like marsupial pocket, and the nipple (represented in black) crowded far down the throat. (After Bresslau.)

while the female expresses milk from her mammary glands down the throat of the helpless fetus by the contraction of the abdominal muscles. Later on, as development advances, the young marsupial draws its milk in the orthodox way.

Oshorn, in *The Age of Mammals*, catalogues 76 genera of marsupials of which 37 are extinct. The living ones, excepting the opossums *Didelphys* of North, Central, and South America, and *Coenolestes* of Central America, are confined to the Australian region. Extinct Eocene genera ranged over what is now Europe, as well as both Americas and Australasia.

It is considered probable that the origin and spread of marsupials occurred before the ancient land bridge that joined Australia to South America had disappeared. Those forms which became isolated at that time in the marsupial Ark of Australia were afterwards able to continue their handicapped existence with comparative success, since they were not brought into competition with the true mammals that developed later on the other great continental areas. Man's introduction of cats, dogs, and especially rabbits into Australia has probably doomed many, if not all, species of monotremes and marsupials of that continent to extinction. As in America, a few species may be able to survive.

It is a striking fact that not only all the native mammals of Australia were monotremes and marsupials, but also that the latter became diversified in much the same way as true mammals into different types adapted to various habitats. The "koala" is a bear-like form. Species resembling wolves, hyenas, cats, rabbits, jumping mice, woodchucks, moles, flying squirrels, and mice are also found in this Order. The kangaroos, *Macropus*; bandicoots, *Perameles*; and opossums, *Didelphys* and *Coenolestes*, are marsupials that suggest cousins among the true mammals to a less degree.

Some of these marsupials are represented in sketches in Figure 55.

c. Subclass EUTHERIA

The eutheria (*eu*, true; *theria*, beasts) include all the other mammals, frequently termed "placentals" because they are characterized by the pres-



Fig. 55. Marsupials. A, Virginia opossum, *Didelphys virginiana*; B, rock wallaby, *Halmaturus*; C, native cat, *Dasyurus*; D, marsupial mole, *Notoryctes*; E, koala, or marsupial bear, *Phascolarctus*, carrying young on back; F, Tasmanian wolf, *Thylacinus*; G, wombat, or marsupial woodchuck, *Phascalomys*. (All from Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. A and B, after Vogt and Specht; C, E, and F, after Brehm; D, after Beddard; G, after Lydekker.)

ence of a *placenta*, formed where the capillary-laden allantois comes into intimate contact with the richly vascularized wall of the uterus (Fig. 34). Here interdigitations of the allantois and uterine wall bring the embryonic and maternal blood streams close together. Across the thin membranes

which separate the two blood streams oxygen and food pass into the blood of the embryo, and waste products from the blood of the embryo to that of the mother. In this manner the placenta forms a functional connection between the mother and offspring throughout the long preparatory life before birth.

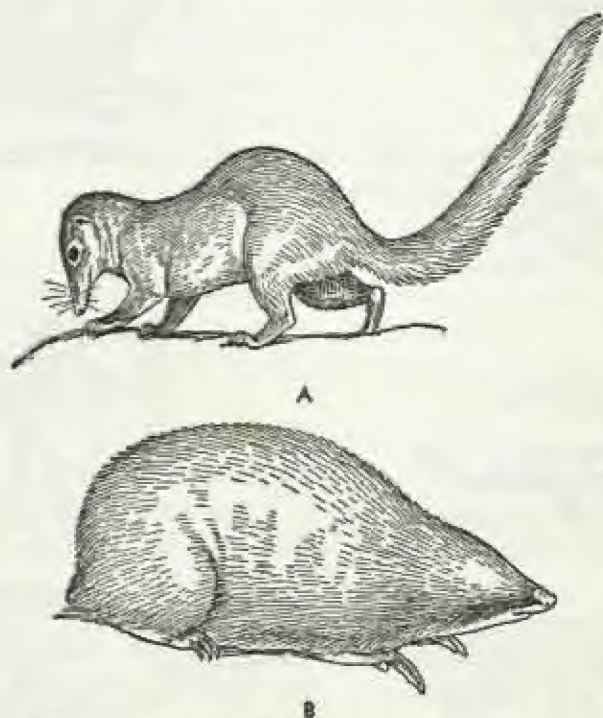


Fig. 56. Insectivores. A, *Tupaia*, the tree shrew, considered by Osborn as near the prototype form of all high placental mammals; B, golden mole, *Chrysochloris*. (From Newman *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. A, after Osborn; B, after Günther.)

Arranged according to the degree of specialization which they exhibit from the most generalized to the most aberrant forms, the orders of living placentals are: INSECTIVORA, DERMOPTERA, CHIROPTERA, CARNIVORA, RODENTIA, PRIMATES, EDENTATA, PHOLIDOTA, TUBULIDENTATA, PERISSODACTYLA, ARTIODACTYLA, PROBOSCIDEA, HYRACOIDEA, SIRENIA, and CETACEA.

A word of identification and comment about each of these orders of true mammals, with examples of a few representative genera, is essential in rounding out a roll call of the vertebrates.

(1) INSECTIVORA.—The insectivores (*vorare*, to eat) subsist largely upon insects, hence their name. They are mostly small, sharp-snouted

animals with leanings towards nocturnal or subterranean life. They include among other genera: the European hedgehog, *Erinaceus*; the moles (Fig. 56B) of which the common mole of the eastern United States, *Scalopus*, and the peculiar star-nosed mole, *Condylura*, as well as *Scapanus* of the Pacific Coast, are American genera; also the shrews, *Sorex*, and the short-tailed *Blarina*, both North American representatives. A few, the tree shrews (Fig. 56A), have retained the primitive mammalian habit of life in the trees. In a number of respects the anatomy of these tree shrews indicates that this group is not far removed from the insectivore stock which was probably ancestral to the Primates.

Osborn names a total of 45 fossil and 34 living genera of insectivores.

(2) **DERMOPTERA.**—The dermopterans, which are without fossil representation, are set aside in an independent Order, although it consists of but a single Genus, *Galeopithecus* (Fig. 57), the "flying lemur" of the Malay region that is an anatomical connecting link between insectivores and bats.



Fig. 57. Flying lemur of Madagascar, *Galeopithecus*. (After Vogt and Specht.)

(3) **CHIROPTERA.**—The chiropterans (*chir*, hand; *pter*, wing), or bats, are mammalian aviators, rather helpless when not on the wing, which fly about at twilight by means of enormously elongated webbed fingers. While the erratic flight of bats is by no means as sustained as the more powerful flight of birds, yet, aided by extremely responsive sense organs, these creatures are unsurpassed in avoiding obstacles while hawking insects in the crepuscular traffic of semi-darkness.



Fig. 58. An insectivorous bat, *Synotis*. (After Vogt and Specht.)

The food of bats in general, and of North American bats in particular, consists practically of insects caught on the wing (Fig. 58). In the Old World tropics the habit of eating fruit has developed on the part of certain large bats called "flying foxes," that live upon figs, guavas, and similar soft fruits.

Another aberrant adaptation in the chiropteran type is presented by the blood-sucking vampires of Central and South America, that have a highly



Fig. 59. Fissipede carnivores. A, Canada lynx, *Felis canadensis*; B, civet cat, *Viverra civetta*; C, spotted hyaena, *Crocuta maculata*; D, gray or timber wolf, *Canis nubilus*; E, raccoon, *Procyon lotor*; F, badger, *Taxidea taxus*; G, otter, *Lutra canadensis*; H, Alaska brown bear, *Ursus gyar*, largest of the bears. (All from Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. B and C, after Beddard; all others after Fuertes.)

modified saclike stomach for the storage of blood which they gorge from some unwilling host. Aside from the unpleasantness of their blood-sucking habits, these bats are under suspicion because they may be agents for the transfer of vicious blood parasites.

Myotis is the common harmless brown bat of cosmopolitan distribution. Of 63 genera of bats in Osborn's list only three are extinct.

(4) CARNIVORA.—The carnivores (*earn*, flesh) have specialized in alertness and brains. They are keen, swift, athletic, gladiatorial killers, feeding by preference upon the flesh of other animals. Their place in the general scheme of things seems to be to keep within limits the prolific rodents that in their absence tend to overrun everything. They also have by their aggressive ways served in the course of evolution as schoolmasters for other mammals, particularly the primates to which man belongs, by stimulating self reliance and resourcefulness. The carnivores are not particularly modified except that the clavicles (collar bones) are reduced or missing and the teeth are somewhat specialized.

They are represented by 73 living and 113 extinct genera in Osborn's list. The suborder FISSIPEDIA (*fissi*, split; *ped*, foot) is made up principally of land animals, while the suborder PINNIPEDIA (*pinna*, fin) comprise fish-eating carnivores that have become secondarily modified for aquatic life.

Among the better known fissipede carnivores (Fig. 59) are the following: *Canis*, dogs, wolves, and coyotes; *Ursus* and *Thalassarcos*, bears; *Felis*, cats, lions, and their kind; *Cynaelurus*, the "cheetah" of India, a kind of cat without retractile claws; and the hyenas, foxes, raccoons, weasels, minks, ermines, skunks, and others.

Among pinnipede carnivora (Fig. 60) are the sea-lions, seals, and walrus.

(5) RODENTIA.—The rodents, or gnawing animals, with 101 living and 61 fossil genera, are the most numerous of all living mammals, particularly as they make up in number of individuals what they lack in size. Their strong, deep-set incisor teeth, which grow continuously throughout life, are self-sharpening chisels. The hard enamel of this type of tooth, confined to the anterior surface, does not wear away as readily as the softer dentine which makes up the bulk of the tooth. Thus a chisel-like, sharp cutting edge of enamel is always maintained. They are prevailing plant eaters and form an important link in nature's chain, since they hand on the sun's energy, stored by green plants, to the carnivores by which they are devoured.

The rodent bloc (Fig. 61) in the Congress of Mammals is represented by the following: *Lepus*, hares; *Sciurus*, squirrels; *Cavia*, guinea pigs; *Sciuropterus*, flying squirrels; *Mus*, rats and mice; and the beavers, musk-



Fig. 60. Pinnipede carnivores. A, Pacific walrus, *Odobenus obesus*; B, male, and C, female, of Steller sea-lion, *Eumetopias jubata*; D, Greenland seal, *Phoca groenlandica*. (All from Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Fuertes.)

rats, porcupines, prairie dogs and woodchucks. By some authorities the rabbits and hares are placed in a separate Order because of their extra pair of incisors and other evidence that they have independently acquired the gnawing habit.

This group is of great economic importance. On the negative side are their destructive habits and possibly disease transmission, such as the carrying of bubonic plague by fleas which may inhabit the fur of rats. On the other hand, several species furnish us with fur or meat and several have been of great value for laboratory experimentation and tests of serums and other material.

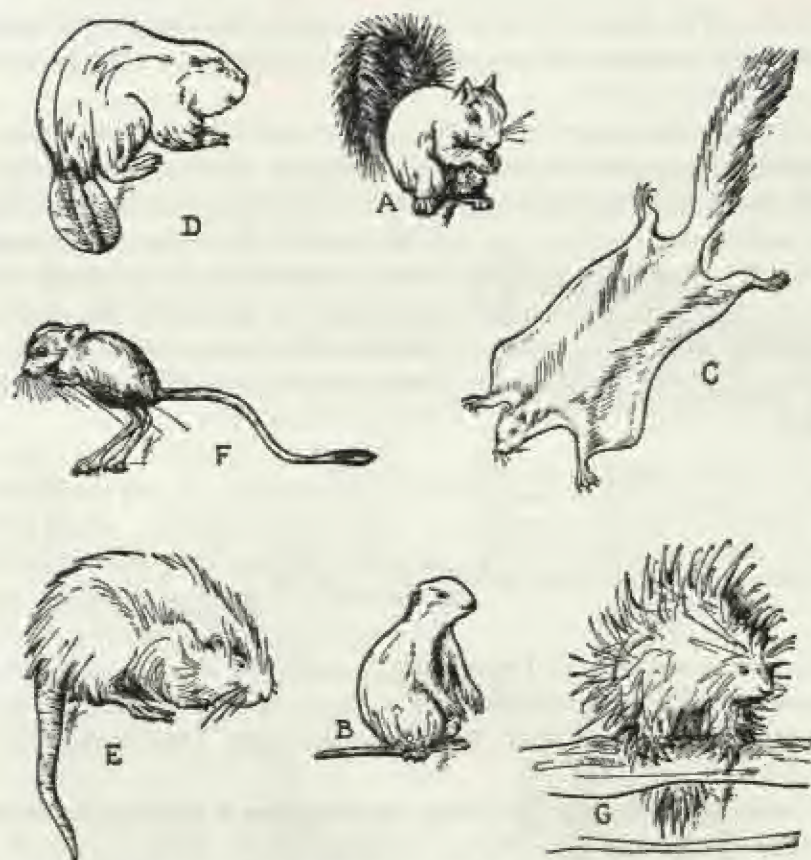


Fig. 61. Representative rodents. A, squirrel, *Sciurus*; B, prairie dog, *Cynomys*. (Both after Dugmore.) C, flying squirrel, *Sciuropterus*. (After Lydekker.) D, beaver, *Castor*. (After Dugmore.) E, muskrat, *Fiber*. (After Carlin.) F, jumping jerboa, *Dipus*, of Europe. (After Beddard.) G, porcupine, *Erethizon*. (After Dugmore.)

(6) PRIMATES.—The primates, including 39 living genera of lemurs, monkeys, apes, and mankind while not so highly specialized in many ways with regard to bodily structure as the several orders yet to be mentioned, stand first in the vertebrate class with respect to brain development. Most of the 23 fossil genera of this order are lemurs, which probably dwelt in trees just as their modern representatives in the forests of Madagascar do to this day. There is considerable evidence that the primates arose from a primitive, tree-dwelling Insectivora stock. Practically all species living today are arboreal, with skeletons not greatly modified from the condition of primitive mammals. Their teeth, also, are comparatively unspecialized but tend to be reduced in number from the 11 pairs of teeth on each jaw of primitive

placentals. The brain and eyes become highly developed, the cerebral hemispheres increasing in size until they completely cover the rest of the brain in higher primates.

Although many travel on all fours, their arboreal habit has resulted in an upright sitting posture that made possible the development of a pair of handy hands and admission to the Manual Training School of the Treetops.



Fig. 62. Smith's dwarf lemur, *Microcebus smithii*. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. After Beddard.)

This was the beginning of a wedgelike vista of possibilities at the broad end of which lies the intellectual life. Organs of defense, like scales, claws, horns, and hoofs, are not needed by primates since wits take their place.

The three suborders are: LEMUROIDEA, TARSIOIDEA and ANTHROPOIDEA.

The *lemurs* (Fig. 62), very primitive, arboreal primates not greatly different from the tree shrews, are found chiefly in Madagascar but with some species in

Africa and Southern Asia. These small animals have an elongate snout and pointed ears. They are covered with a heavy coating of hair. Their big toes and thumbs are set apart from the other digits. Their long tail is not prehensile.

Tarsius (Fig. 63), the only living *tarsioid* genus, is intermediate between the other two primate suborders. A reduction of the olfactory organs and shortening of the snout have permitted a shifting of the eyes forward into a position for binocular vision, although neither eyes nor cerebrum is as well developed as in the monkeys. Like the lemurs they have pointed ears.

In the *Anthropoids* (Fig. 64) the cerebral hemispheres are greatly enlarged and richly convoluted. The eyes are highly developed for increased clarity of vision. The New World monkeys, usually called *Platyrrhines* (*platy*, flat; *rhin*, nose) have broad, flat noses with the external openings directed somewhat laterally. Their thumbs are usually reduced. Their tails are in most cases long and prehensile. Probably the best known member of this group is *Cebus*, the Capuchin monkey, famous as the companion of the hand-organ man.



Fig. 63. *Tarsius spectrum*. (After Haacke.)

The Old World Anthropoids, known as the *Catarrhines* because the external nares are close together and usually open downward (*cata*, down), include three general types: the various African monkeys, macaques, and baboons; the anthropoid apes (belonging to the Family Simiidae); and man. These animals have opposable thumbs. Their teeth are reduced in number to 32. The tail is non-prehensile and frequently greatly reduced. *Macacus* is the lively little monkey so often seen serving time behind the bars in zoölogical gardens and menageries. The rhesus monkey, *Macacus rhesus*, is used extensively in experimental work. The importance of this animal in work on the so-called Rh factor of the blood led to the use of the first two letters of Rhesus as the symbol for the factor.

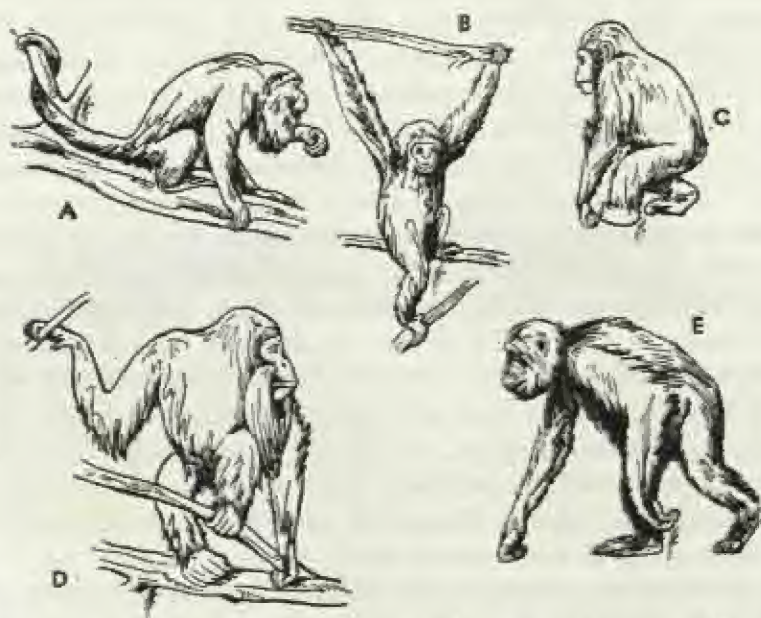


Fig. 64. Anthropoid Primates. A, long-tailed monkey, *Alouatta*; B, gibbon, *Hylobates*; C, chimpanzee, *Anthropopithecus*; D, orang-utan, *Simia*; E, gorilla, *Gorilla*. (E, after Beddard; others, after Schmid.)

The tailless Simians include four genera (Fig. 64). The gibbon (*Hylobates*) is a long-armed, arboreal form of small size, found in the Malay region and neighboring islands. The orang-utan (*Simia*), a native of Sumatra and Borneo, is also a long-armed arboreal type but is considerably larger than the gibbons. The chimpanzee (*Anthropopithecus*) and the gorilla (*Gorilla*), both African forms, have relatively shorter arms than the gibbon or orang. The chimpanzee, primarily an arboreal form,

spends some of its time on the ground. The gorilla, essentially a ground dweller, is the largest and most powerful of all apes. Both chimpanzee and gorilla exhibit some degree of intelligence and reasoning power of the human type. Of the attempts to educate these apes, the most successful ones have been those using chimpanzees. They can be taught to wear clothing, dine at a table, ride a bicycle, act in moving pictures, smoke a pipe, expectorate with precision, and perform many other acts characteristically human.

Modern man of whatever race or color belongs zoologically to a single genus and species, *Homo sapiens*, Linn., although the name "wise man" is more appropriate for some individuals than for others. Although similar to Simiidae in most respects, man differs from them in some structural details. He is more erect, has shorter arms and relatively larger thumbs. The big toes of the apes are opposable but in man these toes are in line with the others. While the simians have powerful teeth set in heavy jaws, man has smaller front teeth and tooth-bearing regions of the jaws. Consequently man has a chin. The supraorbital ridges over the eyes are much less pronounced in man. The human cerebrum is distinctly larger, in part due to the considerable development of the frontal lobes where the speech centers are located. Room for these anterior lobes is provided by a raised front part of the skull which gives the higher forehead region. These differences are chiefly associated with man's mental development, speech and ground-dwelling habits.

The fossil representatives of man will be considered in a later chapter. Together with modern man all are included in the family *Hominidae*.

(7) EDENTATA.—The edentates (Fig. 65c and d) are rather degenerate mammals, either toothless as the name implies, or with poor chalky teeth. Their center of distribution is South America, for all of the 15 living genera are found there, although the anteaters, *Tamandua*, *Myrmecophaga*, and *Cyclopes*, extend as far north as Central America and Mexico, and the nine-banded armadillo, *Dasypus novemcincta*, even into Texas. Of the 34 genera of fossil edentates, four are from North America, three from both North and South America, and twenty-five exclusively from South America. Thus it is evident that the center of distribution of this order is South America.

The topsy-turvy sloths, *Bradypus* (three-toed), and *Choloepus* (two-toed), are well named because of their sluggish habits. They are awkward defenseless creatures clothed with coarse gray hair and equipped with long hooklike claws which enable them to hang upside down in the branches of tropical trees, where they depend upon their resemblance to motionless

masses of "gray-beard mosses" for protection from their carnivorous foes. Sidney Smith said of them: "Sloths live suspended, and sleep suspended, and in fact, pass their whole lives in a state of suspense, like a young curate when he is distantly related to a bishop."

Of the armadillos, besides the nine-banded one already mentioned, there is the six-banded *Dasypus sexcinctus* of Paraguay and Brazil, and the three-banded *Tolypeutes*. Some of these can roll up in their scaly armor like "pill bugs" when danger threatens, presenting a hard nut for any predaceous foe to crack.



Fig. 65. Representatives of the "edentate" Orders. A, scaly anteater of Africa, *Manis*, belonging to the Pholidota; B, armadillo of Africa, *Orycteropus*, belonging to the Tubulidentata; C, three-toed sloth of South America, *Bradypus*, and D, six-banded armadillo of South America, *Dasypus*, both belonging to the Edentata. (A, after Beddard; B and C, after Schmid; D, after Brehm.)

The extinct giant armadillo, *Glyptodon*, which was encased in an armor without bands that would enable it to roll up, was, however, so well protected that, like a war tank, it did not need to imitate a pill bug. In spite of their armor these giants became extinct and their fossil remains are an eloquent memorial to the fact that something more than passive resistance is necessary in order to maintain a species on the earth.

(8) PHOLIDOTA.—The pholidotes include two genera, *Manis* and *Pholidotus*, the pangolins or scaly anteaters (Fig. 65A) of Africa and Southern Asia. They have elongate heads with long, very protrusible tongues with which they pick up termites. No teeth are present. Their bodies are covered with large, horny, overlapping scales. Powerful, sharp claws are present, especially on the front feet. Although long grouped with the

edentates, these animals are more properly placed in a separate order for geographical as well as anatomical reasons.

(9) TUBULIDENTATA.—The tubulidentates, formerly placed among the edentates, include a single species of the genus *Orycteropus*, the practically hairless aard-vark of the South African Boers (Fig. 65b). This animal has the long snout, long tongue and powerful claws of a termite eater. Its teeth, without enamel, have a perforated dentine.



Fig. 66. Perissodactyl ungulates. A, wild ass of Syria, *Equus onager*; B, tapir of South America, *Tapirus*; C, two-horned rhinoceros of Africa, *Rhinoceros bicornis*; D, one-horned rhinoceros of India, *Rhinoceros indicus*. (All after Beddard.)

(10) PERISSODACTYLA.—The perissodactyla (*perissos*, odd-numbered; *dactyl*, finger, toe) are large, herbivorous ungulates (*ungula*, hoof) which walk on the hoofed tips of an odd number of digits. Their molariform teeth have large chewing surfaces usually bearing high cross-ridges which greatly increase the effectiveness of the teeth in grinding grass, leaves and other vegetable matter. In all of these animals, the main axis of each appendage passes through the third digit, which therefore carries most of the weight.

The tapirs (Fig. 66b) of South America and the Malay region have probably retained more of the general features of the ancestral stock of the Order than have any other members. They have four toes on the front feet (thumbs missing) and three on the hind feet (big and little toes missing). Their practically complete dentition includes relatively generalized molariform teeth. Among their specializations is a short proboscis formed by a slight elongation of upper lip and nose.

The rhinoceros (*rhino*, nose; *ceros*, horn) group (Fig. 66c and d) includes several species of large, awkward animals with three toes on the hind feet and three or four on the front ones. On the top of the snout, in the mid-line, they have either a single horn or two, one behind the other. Each horn is really a mass of hairs stuck together.

The horses (Fig. 66a) are characterized by the reduction of their digits until only one (the third) is in contact with the ground while two others (the second and fourth) are small splints at the base of the functional toe. All living species of horses, including their close relatives the asses and zebras, belong to the genus *Equus*. These animals have perhaps the most definitely traced pedigree of all mammals. Their record goes all the way back by successive links to *Eohippus*, a small Eocene ancestor about the size of a fox that had four toes on the front feet and three on the hind feet, as do present-day tapirs and some rhinoceroses.



Fig. 67. Non-ruminant artiodactyls. A, peccary of South America, *Pecari*; B, wart hog of Africa, *Phacochoerus*; C, *Hippopotamus* of Africa. (All after Beddard.)

(11) ARTIODACTYLA.—The artiodactyls (*artios*, even-numbered) are large, herbivorous ungulates with molariform teeth similar to those of perissodactyls. In these animals, however, the main axis of the leg passes between the third and fourth digits which usually bear equally the weight of the animal. The first digit (thumb or big toe) has disappeared and usually the second and fifth digits are considerably reduced.

The pigs (genus, *Sus*), peccaries, wart hogs of Africa, and hippopotami use all four toes and have simple stomachs and no horns (Fig. 67). They are not limited to a diet of plants but will also eat flesh.

All the other artiodactyla are ruminants (*ruminare*, to chew over again), so called because they first swallow their food whole, then regurgi-

tate it at their leisure, and thoroughly chew it (Figs. 68 and 69). The small balls of food returned to the mouth are known as cuds. Strictly herbivorous, they have three- or four-chambered stomachs adapted to their cud-chewing habits. They use only their third and fourth digits. Many are provided with defensive horns, either hollow and permanent, like those of the cow, or solid and periodically shed and renewed like the antlers of a stag. Among the better known members of this group are: the camels and dromedaries (*Camelus*); the South American llamas; the giraffes (*Giraffa*); the deer,

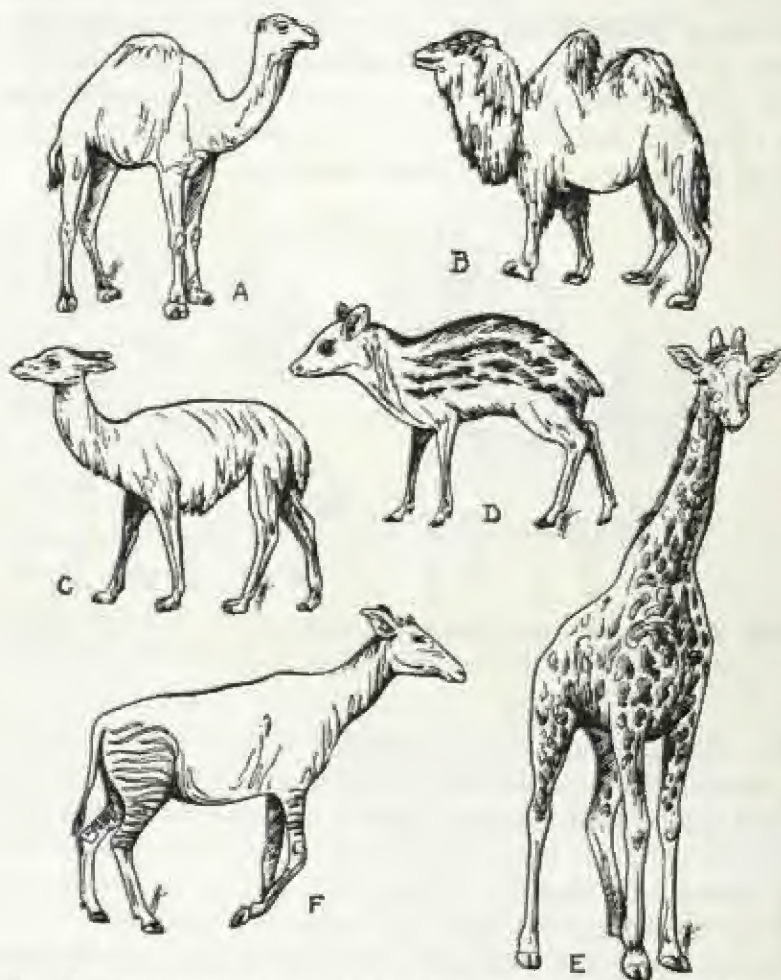


Fig. 68. Representative ruminants. A, dromedary, *Camelus dromedarius*. (After Schmid.) B, camel, *Camelus bactrianus*. (After Beddard.) C, llama of South America, *Auchenia*. (After Beddard.) D, chevrotain of India, *Tragulus*. (After Beddard.) E, giraffe, *Giraffa*; F, okapi, *Okapia*. (After Schmid.)

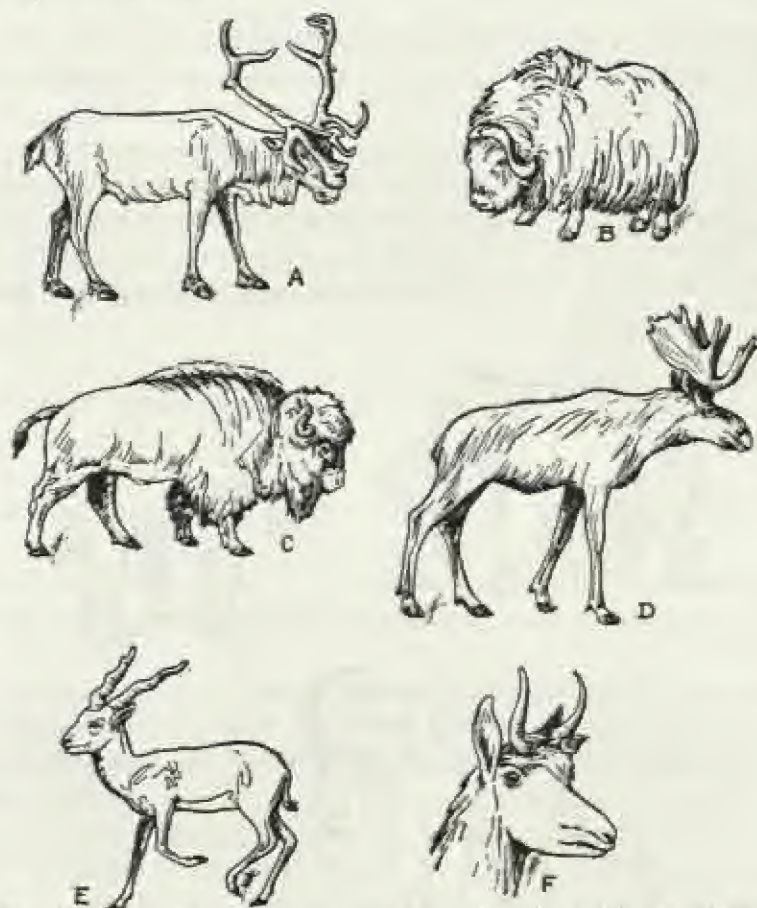


Fig. 69. Horned ruminants. A, reindeer, *Rangifer*. (After Beddard.) B, arctic musk ox, *Ovibos*. (After Schmid.) C, American buffalo, *Bison*; D, moose, *Alces*. (After Beddard.) E, antelope, *Antilopa*. (After Schmid.) F, pronghorn antelope, *Antilocapra*. (After Dugmore.)

elks, moose, and similar forms; sheep (*Ovis*); goats (*Capra*); and domestic cattle (*Bos*).

Ogden Nash has described the common cow as follows:

"The cow is of the bovine ilk,
One end is moo, the other milk."

The artiodactyls and perissodactyls are of great economic importance to man. They furnish us with portions of our clothing, transportation, food—including milk and much of our meat—and serums so important in fighting disease.

(12) PROBOSCIDEA.—The proboscideans are the elephants, largest of living land animals, which are so bulky that they are obliged to walk stiff-

legged in order to support their tremendous weight (Fig. 70). The heavy head is sustained horizontally by a short stout neck, and the rigidity brought about by this arrangement, as well as by the stiff uncompromising pillar-like legs, is compensated by the development of a "trunk," a combination of the nose and the upper lip enormously drawn out into a flexible prehensile organ (*proboscis*). Each of their five digits terminates in a hoof-like structure. Their molariform teeth reach the extreme of development of the grinding cross-ridges. Their upper incisors are greatly enlarged into long tusks.



Fig. 70. Proboscidea. A, extinct mammoth, *Elephas primigenius*. (After Schmid.) B, restoration of an extinct dinotherium, *Dinotherium giganteum*. (After Abel.) C, African elephant, *Loxodonta*. (After Schmid.)

Some proboscideans, such as the mastodons and the hairy mammoths of the Ice Ages, became extinct in comparatively recent times, geologically speaking, while other less-specialized ancestors, as *Dinotherium* of Europe and Asia, and *Palaeomastodon* of Egypt, are considerably more ancient.

There are two genera of living proboscideans: *Elephas*, the small-eared Asiatic elephant; and *Loxodonta*, the large-eared African variety. The former species has been domesticated in India for a long time. One famous individual, "Jumbo," weighed $6\frac{1}{2}$ tons and was 11 feet high. For years this gigantic beast entertained thousands of children, young and old, under Barnum as impresario. Jumbo's monumental skeleton stands in the American Museum of Natural History in New York.

(13) HYRACOIDEA.—The hyracoideans are coneys or “rock rabbits,” which, according to the Book of Proverbs “are but a feeble folk, yet they make their homes in the rocks.” They are small cud-chewing animals, superficially resembling guinea pigs, with hooflike tips to their toes, of which there are four on each front foot and three on each hind foot. They were probably derived from the same basic stock as the proboscideans and the sirenians. They include two genera: *Dendrohyrax* (Fig. 71) of Africa, and *Procavia* of Syria and Arabia.



Fig. 71. African coney, *Dendrohyrax*. [After Beddard.]

Because of certain anatomical similarities the last four Orders just mentioned (Perissodactyla, Artiodactyla, Proboscidea, and Hyracoidea) may be artificially grouped together as the ungulates or hoofed mammals. Hoofs have probably appeared independently in the different orders. For the most part they are large, rather stolid, plant-feeding creatures, most at ease when standing up on their highly specialized feet which are adapted for bearing continuous weight by being encased in shoelike hoofs. Unlike the soft-footed carnivores that collapse into a reposeful recumbent posture at every opportunity only to spring into alert activity upon the slightest incentive, ungulates never sit down and do not lie down without considerable deliberation and effort.

The 73 genera of ungulates include many kinds of great utility to man. They have also played a notable role in the past history of the world, as evidenced by the fact that 204 genera of fossil ungulates are known, many more than of any other order of mammals. These numbers are no doubt due in part to the readiness with which this group of animals has left fossil evidence of a former existence.

(14) SIRENIA.—The sirenians, although of very different external appearance, have certain unmistakable anatomical affiliations with elephants and vegetarian ungulates. They are large clumsy water animals having a broad snout covered with sparse coarse bristles and an otherwise hairless skin. The anterior legs are modified into swimming flippers, while the hind legs are entirely absent.

They are perhaps the animals that have furnished the slender basis of fact from which imaginative sailors from time immemorial have spun tales of mythical mermaids and sirens. A less romantic but more apt common name for them is “sea cows.”

Of this order only two genera (Figs. 72 and 73) are represented by living animals, that are separated from each other on the globe about as far as it is possible, since "manatees" representing the genus *Trichechus* inhabit the rivers of the northeastern coast of South America and beyond as far north as the Everglades of Florida; while the "dugong," *Halicore*, lives in the Red Sea and Indian Ocean.



Fig. 72. Atlantic sea cow or manatee, *Trichechus*. (After Dugmore.) Fig. 73. Dugong, or Indian Ocean sea cow, *Halicore*. (After Schmid.)

Of the 7 fossil genera, one, *Rhytina stelleri*, or Steller's sea cow, has been extinct less than 200 years. This species first became known in 1741 when Steller, a Russian whaler, was shipwrecked upon a small group of islands in Bering Sea. He was saved from starvation by finding a rookery of these large sea cows upon which he and his crew fed until rescued. During the following quarter of a century Russian whalers with human greed and stupidity hunted these valuable food animals to extinction, for Nordenskiöld, who visited the islands in 1768, reported that the last individual of the colony had been killed. This species of sea cow has never been found elsewhere.

(15) CETACEA.—The cetaceans, or whales and their allies, among which are to be found the largest animals that ever lived, include the leviathans of the oceans. The ancestry of the cetacea is a puzzle for the solution

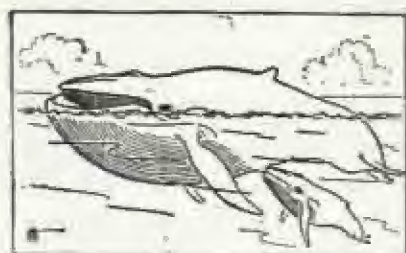


Fig. 74. Humpback whale suckling her young. (After Scammon.)

of which fossils give scanty aid. Comparative anatomy shows that they bear unmistakable hall-marks of mammalian forbears, such as breathing air by means of lungs and feeding the young upon milk. Since the mammalian plan undoubtedly originated with land forms, cetaceans must have undergone profound modification

in order to become adapted secondarily to a marine existence where their great weight could be supported in water. By reason of their warm-bloodedness and a thick blanket of heat-retaining blubber under the skin.

these gigantic animals are able to pursue their activities even in Arctic waters.

While in the act of nursing, which is obviously accomplished under difficulties, the young whale presents a curious resemblance to a small tug attached to the side of an ocean liner (Fig. 74).

Whales may be grouped into two suborders; ODONTOCETI, or toothed whales that feed primarily upon fishes, and MYSTACOCETI, or whalebone whales which, by means of a peculiar brushlike device of "whalebone" in the cavernous mouth cavity, strain out and swallow countless myriads of microscopic ocean inhabitants, that constitute for them a nutritious "sea soup" of unlimited supply.

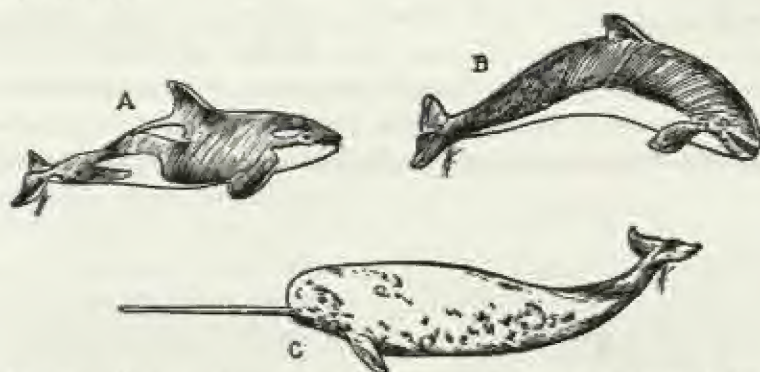


Fig. 75. Odontoceti, or toothed whales. A, killer whale, *Orca*; B, porpoise, *Phocaena*; C, narwhal, *Monodon*. (A, after True; B and C, after Schmid.)

The toothed whales (Fig. 75) are usually not of extraordinary size and frequently forage about in their watery hunting grounds in schools. Some of them are: *Delphinus*, the dolphin; *Phocaena*, the porpoise; *Grampus*, the grampus; *Orca*, the killer; *Monodon*, the narwhal, with a single enormous twisted tooth projecting horizontally in front like a pikestaff; *Physeter*, the sperm whale, with teeth only in the lower jaw; and *Hyperoodon*, the bottle-nosed whale. The last two attain considerable size.

Examples of the giant whalebone whales are: *Rachianectes*, the gray whale; *Balaenoptera*, the blue or sulphur-bottomed whale; *Megaptera*, the hump-backed whale; and *Balaena*, the right whale (Fig. 76). The blue whale is reputed to reach a length of 100 feet and a weight of perhaps 150 tons.

There are 9 genera of fossil cetaceans, and 27 genera of living ones, some of which are becoming scarce because they have been so relentlessly hunted by man.

Speaking of whales, John Godman a century ago wrote the following perfect apology for those travelers who return from foreign lands with tall stories to tell to those who stay at home: "Large as the size of the whale



Fig. 76. Right whale, *Balaena*. (After Schmid.)

certainly is, it has been much over-rated; for such is the avidity with which the human mind receives communications of the marvellous, and such the interest attached to those researches which describe any remote and extraordinary production of nature, that the judgment of the traveller receives a bias, which, in case of doubt, induces him to fix upon that extreme point in his opinion which is calculated to afford the greatest surprise and interest."

The Distribution of Animals in Space— Chorology and Ecology

I. THE POINT OF VIEW

An observant traveler going from home in any direction gradually leaves behind a familiar world of animals and plants and, if his travels are sufficiently extensive, arrives in a land of strange organisms for the most part quite unlike those he already knows. He discovers that no one kind is to be found everywhere, but that each kind has its own home territory beyond which it does not ordinarily venture. In imagination he might map out upon the globe the home patch, with all its irregular boundaries, which each of the 600,000 or more species of living animals occupies. Such a map would be exceedingly complex because the areas thus delimited would not only be very unequal in size but would also

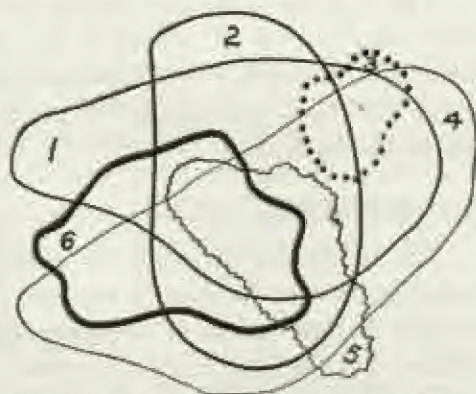


Fig. 77. Hypothetical limits of the distribution of six different species of animals, arranged in superimposed areas.

overlap each other in a great variety of ways like a gigantic palimpsest. A diagram to express this idea, in which the areas of only six instead of 600,000 species are involved, is shown in Figure 77.

Such a picture, moreover, if truly represented, would not be definite and fixed but would be a *motion picture*, presenting constant change like a rotating kaleidoscope, since the frontiers established by living things can never remain constant. It is well known that animals in the past occupied territory from which they are absent today, and that the contrary is equally true.

Evidence from fossils, for example, shows that at one time tropical parrots and, at another, arctic reindeer were natives of what is now temperate France; that elephants formerly roamed over the United States; and antarctic albatrosses flew over England. Just as history records a succession of civilizations, so plant and animal life, past, present, and future, presents a shifting scene.

The *locality* where any species of animal is found is as much a diagnostic characteristic of the kind of animal in question as its peculiarities of structure or behavior. It follows that any kind of fossil or living form loses much of its value for the scientist if the place it comes from is unknown.

II. ECOLOGY AND CHOROLOGY

The comparatively new biological science of *Ecology* (*oikos*, home; *logos*, discourse) deals with the intimate arrangement and behavior of organisms within their respective habitats. Ecology may be defined as "scientific natural history."

The province of the more inclusive science of *Chorology* (*choros*, place; *logos*, discourse) is to determine the general distribution of animals and plants over the earth and to discover the why and wherefore of their occurrence. Chorology is a science for the traveler, while ecology is the science for the stay-at-home.

III. HABITATS

The immediate surroundings in which any animal is "at home" are called its habitat. In general animals are said to occupy either a land or a water habitat. Some of the more specific descriptive terms applied to habitats are: desert; forest; mountain; subterranean; prairie; meadow; marsh; pelagic; abyssal; pond; marine; fluvial; and estuarial. This list of descriptive local areas may be almost indefinitely extended according to the minuteness with which the details are scrutinized.

The arrangement of these various kinds of habitats over the surface of the globe determines to a large extent the distribution of living forms. It is obvious, for instance, that arboreal animals are not to be expected in the open ocean, which constitutes about three fourths of the entire surface of the globe, and much less are fishes to be discovered in waterless deserts.

Animals found living successfully in any habitat must be measurably adapted for life conditions there, although there are many cases in nature of imperfect adaptation where a square peg is attempting to fill a round hole, and *vice versa*. The usual result in such a misfit is that the peg either explores until it finds its proper hole, or gradually changes to fit the hole

that it is in. Both hole and peg are changeable things but the initiative of change belongs not to the hole but to the peg.

Any habitat is not occupied by all the animals and plants adapted to live in it. The prevalent idea, for example, that climate determines the distribution of organisms is largely erroneous. There are no grizzly bears in Switzerland, no birds-of-paradise in California, and no "snakes in Ireland," although the climate in each case is suitable for the absentees. The equatorial forests of Africa and South America have practically the same climate, yet the former region is characterized by elephants, apes, leopards, giraffes, and guinea fowl, while the latter has none of these animals but does support tapirs, long-tailed monkeys, jaguars, and toucans, which are never found in Africa.

So long as mankind was satisfied with the naïve supposition that the earth has been arbitrarily populated by independent acts of special creation, much as a person might arrange chessmen upon a board, there was no sense nor object in developing a science of chorology. There was nothing to explain. Leopards, for example, were in Africa and jaguars in South America because they were placed there, newly made, in the beginning. The two kinds of large cats were entirely independent in origin and without any relation to each other. When men developed the conception, culminating with Darwin, that all organisms are more or less related to each other as descendants of common ancestors, and that every species arose in the course of time by modification from some other species, then the *manner of distribution* over the earth became full of significance, seriously challenging the attention of thinking people.

IV. THE LAWS OF DISTRIBUTION

Three laws governing the distribution of animals were formulated by Jordan and Kellogg in *Animal Life*. These laws may be stated as follows: *Every species is found everywhere unless* (1) it was unable to get there; (2) having "got there," it was unable to stay; or (3) having arrived, it became modified into another species. It will be profitable to consider these laws briefly.

First, it is not the *suitability* of a habitat so much as its *accessibility* from a place of origin, that determines the presence of an inhabitant. For instance, there are no hummingbirds in Africa, while there are over 450 species in South and Central America, not because Africa itself is unfavorable to hummingbird occupation, but because these tiny fairylike creatures have never been able to cross the wide oceans separating their ancestral American home from faraway Africa.

Second, there are many instances of animals and plants that have succeeded in invading new territory, but have been unable to hold their own there. Not all pioneers become settlers. At one time our federal government introduced a herd of camels after an adventurous sea voyage into the semi-arid region of the Southwest, and allowed them to run wild in the hope that they would multiply, spread, and eventually form a valuable addition to a region inhospitable to most large animals. The environment was very like that from which the animals came and the experiment might have proved successful but, as has been asserted, for the unfortunate fact that local cowboys, with little regard for consequences, had so much sport periodically rounding them up and putting them through their paces, that the strange incongruous beasts were literally worried to death.

Third, successful invaders may win out in occupying new territory at the expense of their own specific individuality. They are the adaptable round pegs thrown into new habitats of square holes, that nevertheless remain and square themselves to fit the new holes. They are the immigrants that have deserted the ways of their mother country and become naturalized in the land of their adoption. A classical illustration of cases of this kind, cited by Darwin in *The Origin of Species*, is that of animals upon the Galapagos Islands off the northwest coast of South America. Of 26 species of land birds found upon these islands, 23 species are similar to, but still specifically different from, those inhabiting continental land a few hundred miles away. The interpretation given by Darwin is that when the Galapagos group was separated from the mainland in recent geological times, a new habitat was formed in which various individuals of continental species were isolated. Each of these 23 species, changing gradually under the molding influence of isolation, grew to be sufficiently different from its original mainland ancestors and cousins to rank as a different and distinct species. These facts so impressed Darwin that he began to think about the *origin of species*, with the fortunate result that subsequently a great many other people were induced to think about the same subject.

To these three laws of distribution may be added a fourth, namely: *Each species originated historically from some preceding species at some definite place, and its present distribution is the result of two opposing forces, EXPANSION and REPRESSION.*

V. MALTHUS' LAW OF OVERPOPULATION

It would be as impossible for an unrestrained gas to remain in one place, as for any species of animals or plants to forego the attempt to occupy unoc-

cupied territory to which it has access. The reason for this is the enormous possibilities of expansion inherent in the reproductive processes of all organisms, a condition formulated by Malthus (1766-1834) in his "Law of Overpopulation." For example, when a single codfish produces 9,000,000 eggs in one season, it is obvious that infant mortality must come to the rescue, else in a few generations every available inch of space in the ocean would be preempted by codfish. Even slow-breeding animals like elephants, which produce perhaps six young in a lifetime of a hundred years, would, according to Darwin, require less than 800 years to produce from a single pair nearly 19,000,000 elephants. Allowing 20 feet of space for each elephant, this would make a continuous parade, which would have delighted Barnum, reaching nearly three times around the world at the equator. Elephants and codfish, however, do not multiply out of all bounds as the above theoretical figures suggest, for the expansive forces of reproduction are kept in control, year in and year out, by opposing repressive factors which maintain a balance in nature.

VI. FACTORS INDUCING EXPANSION

1. The Food Problem

Somewhere in one of his delightful essays, Dr. Samuel McChord Crothers presents the illuminating statement that "the haps and mishaps of the hungry make up natural history." There is no doubt that the insistent need for food, as expressed by hunger, is a mainspring of animal activity that, like a centrifugal force, compels animals to go forth in the quest of what they may devour. Even among higher animals which exercise parental care, there comes a time when the young may expect no longer to share food with their parents but must seek fresh pastures. To illustrate with a botanical instance, it would be disastrous if the acorns produced by an oak tree all remained to grow up within the parental circle.

Not only is there competition for food and place among animals and plants of a kind, but there is also severe rivalry between different kinds of creatures for the same food supply. The miscellaneous company which at any time sits at Mother Nature's table, does not always, or even often, observe the restrained table manners of polite society, so that there is every inducement to go elsewhere.

2. Change of Habitat

Another general factor that causes organisms to spread, is change in the habitat occupied. Such a change may be temporary, like the drying up of

ditches and streams that affects aquatic organisms, or it may be permanent, like deforestation at man's hands, which leaves arboreal animals homeless and leads to flood conditions.

It may be sudden and catastrophic, like a prairie fire or a flood, forcing all sorts of animals to flee at once for their lives; it may be gradual like the change of seasons, when winter succeeds summer; or it may be so very slow that it extends over generations in time, like the relentless dawn of a glacial period.

In all cases, however, when an environment becomes unfavorable, there are at least four alternatives open to the inhabitants: (1) organisms may simply succumb to the environmental change, completing their normal life cycles before the unfavorable conditions befall, as in the case of annual plants and most insects; (2) they may retire from active life and mark time while temporary unfavorable conditions last, as do hibernating animals and encysting protozoans, or trees that shed their leaves in winter and "hold their breath" until spring; (3) they may remain plastic enough to change themselves as the environment changes, thus keeping pace by adaptation to new conditions; or (4) they may forsake unlivable surroundings and seek a more favorable place to carry on, like migrating birds, grasshoppers, and emigrants of all kinds. This latter alternative of migration, brought about by change in the habitat, plays an important rôle in the distribution of animals and plants.

VII. MEANS OF DISPERSAL

The ways and means, direct and indirect, that are employed by organisms for dispersal, furnish a fascinating chapter in natural history. Only a few of the most common agents may be mentioned here.

Among plants *wind* is an important agent. In many instances seeds are rigged with ballooning or parachuting devices, or are so light as to be easily borne upon currents of air. The tiny dustlike seeds of certain orchids, for instance, have been known to float in air from Holland across the North Sea, while molds testify to the efficiency of air movements in scattering spores of these ubiquitous organisms everywhere.

Over 60 species of North American birds have been reported, which have reached Europe and become established there by being borne out of their migratory routes by winds, while flying insects like grasshoppers are frequently assisted in their widespread movements by air currents.

Water furnishes another highway for travel. The uneasy tides keep the congested inhabitants of the seashore constantly stirred up and on the move,

while flowing streams and ocean currents act continually as agents in the involuntary transfer of all sorts of organisms from one place to another. Even floating *icebergs* are precarious rafts upon which stray arctic animals are sometimes borne some distance into new regions.

Animals themselves assist each other in dispersal in a multitude of ways, as stowaways, kidnappers, and "thumbies." The larval *glochidia* of certain sluggish fresh-water clams of the genera *Unio* and *Anodonta*, fasten themselves to the gills of swiftly moving fishes, thus stealing a ride to some distant point in the stream where they detach themselves and set up their semi-stationary housekeeping in a new place. Parasites naturally go wherever their hosts go, and so are introduced into the society of new hosts. Animals are particularly useful agents in scattering the seeds of plants. "Sticktights" and burrs of all sorts are makeshifts on the part of plants to steal a ride by attaching to passing animals. Seeds of various kinds too are embedded in attractive fruits with the result that they are eaten by animals and so deposited in some new locality after passing unscathed through the digestive tube of the traveling host. Thus cherry bushes are planted beneath a wood thrush's nest, and fences along the waysides are draped with poison ivy by feathered conservationists.

The mistletoe, which grows parasitically as an air plant attached to the bark of trees, presents an extreme instance of distribution through animal agency. Doves eat the seeds of the mistletoe, because they are encased in alluring sticky berries. Frequently it happens, much as when the traditional small boy emerges from the jam closet, that remains of the feast adhere around the margin of the mouth. The dove flies away to another tree where it performs its toilet by wiping a sticky beak, with the adhering seeds, upon a branch. The seeds are wiped off in this way and stuck to a fresh branch in the exact location favorable for the growth of a new epiphytic plant in a new place.

Of all animals *man*, however, has probably done more than any other in furthering the spread of organisms. In many instances this has been done intelligently and to the ultimate benefit of man himself, as in the case of cultivated plants and domesticated animals. The biological landscape has been changed almost everywhere by the transforming hand of man. Crops of various kinds dot the surface of the globe where wilderness once flourished, while introduced flocks and herds roam in safety over territory once the possession and battleground of native wild animals.

Frequently man has made serious mistakes from the human standpoint in meddling with the balance of nature. The introduction of that over-successful "avian rat," the English sparrow, into the society of American

birds has been many times regretted by man on account of injury to native birds with which it comes into competition. The bloodthirsty mongoose, that was brought to Jamaica and also to Hawaii to kill rats infesting sugar cane fields, proved to be an efficient rat exterminator, but it went further and destroyed other animals, particularly chickens. As a result poultry-raising in these islands has been seriously interfered with, and now a price has been set on the head of every mongoose.

Several years ago a gentleman in Medford, Massachusetts, who conceived the idea that some more hardy insect than the silkworm might be found to spin silk, and at the same time feed upon less restricted food than mulberry leaves, brought back from Europe a few gipsy moths, *Porthetria dispar*, to use in experiments. The box in which they were contained, so the story goes, was accidentally knocked out of an open window and some of the moths escaped, but for the time the incident was forgotten. This was in 1869. By 1889 the descendants of these chance immigrants had prospered to so great an extent that the people around Medford became alarmed and a town meeting was held at which \$300 was appropriated to fight the pests. "In that summer," the record shows, "the numbers were so enormous that the trees were completely stripped of their leaves, the crawling caterpillars covered the sidewalks, the trunks of the shade trees, the fences, and the sides of the houses, getting into the food and into the beds." Dr. Lutz in his *Field Book of Insects* published in 1921 wrote: "Millions of dollars have been spent in an effort, so far unsuccessful, to free us from the invader, and the most that has been done has been to confine it to New England."

The white cabbage butterfly, *Pieris rapae*, first came to America from Holland in a sloop load of wormy cabbages landed at Quebec in 1861. Twenty years later, according to the Department of Agriculture at Washington, it had colonized America on the Atlantic Coast from Hudson's Bay to Florida. In 1886 it had arrived at Denver, and in 1900 had reached the Pacific Coast, having accomplished the conquest of the entire United States and a part of Canada in less than thirty years.

Shipworms, *Teredo*, on the outside of the hulls of vessels, and rats on the inside have spread themselves the world over wherever shipping has gone. In 1827 mosquitoes, traveling as "wrigglers" in the bilge water of a sailing vessel, arrived at the Hawaiian Islands. They have prospered since then and made the Islands their own.

Several years ago a marble statue, made by the sculptor Thorwaldsen in Italy, was set up in Copenhagen. It is said that, as an accidental result, twenty-five species of Italian weeds, the seeds of which were in the straw packing around the statue, made their appearance in the immediate vicinity.

Similar instances of the effects of the interference of meddlesome man with the natural arrangement of organisms in space could be indefinitely multiplied.

VIII. FACTORS OF REPRESSION

Among various factors which hinder world conquest on the part of any single species of animals or plants, are: (1) inadequate means of dispersal; (2) non-adaptability to new conditions; and (3) barriers of different kinds.

1. Inadequate Means of Dispersal

The difficulties of "getting there" are not especially apparent in the case of free-moving animals like birds and insects. They become very real, however, as well as serious for many organisms whose structure is not particularly adapted for locomotion over considerable distances, yet the race is by no means always to the swift. The story of the tortoise and the hare finds plenty of parallels in nature.

When Gould, with his searching eye for mollusks of all kinds, wrote *A Report on the Invertebrata of Massachusetts* in 1841, he made no mention of *Littorina litorea*, a small familiar periwinkle that at present is one of the most abundant species of snails along the Atlantic Coast. In 1855 Morse found a few of these animals in the Bay of Chaleur at the mouth of the Saint Lawrence river, which had been accidentally brought over in ballast from their original home in Europe. By 1875 Verrill reported *two* as a rare find at Woods Hole, Massachusetts, several hundred miles to the southward, and in 1880 Smith found the first one to be noted as far south as New Haven, Connecticut.

Another example of the surprising spread of an animal handicapped by poor methods of locomotion is that of *Sagartia luciae*, a small semi-transparent sea-anemone that lives attached to stones in the tidal zone. It was discovered at New Haven by Verrill in 1892, who named it *luciae* in honor of his daughter Lucy. In 1895 it was reported at Newport, R. I.; in 1898 at Woods Hole, Mass.; in 1899 at Nahant, Mass.; in 1901 at Salem, Mass.; and in 1903 at Cold Spring Harbor, Long Island, N. Y., where it is now abundant. Thus this "stationary" animal spread itself over several miles of coast line within a single decade.

2. Non-adaptability to New Conditions

The non-adaptability of organisms to new habitats, which they may have invaded, is doubtless much greater than appears on the surface, for it

surely acts as a deterrent to their spread. Successful invaders that gain a new foothold and retain it catch the eye and claim attention, while unsuccessful ones which reach the Promised Land but are unable to establish themselves there, escape attention and pass unnoticed.

Many plants that thrive under cultivation, like maize or Indian corn, appear to be unable to maintain themselves in nature when by chance they are allowed to run wild.

The yellow fever mosquito, *Stegomyia fasciata*, fortunately does not succeed north of a certain dead-line, although no doubt it has repeatedly crossed this invisible limit, like the English ivy that clothes the walls of southern buildings in luxuriance, but fails to grow well in more northern situations, in spite of being repeatedly planted and nurtured there.

3. Barriers

Barriers which check or stop organisms on all sides are at least three in kind: PHYSICAL, GEOGRAPHICAL, and BIOLOGICAL.

Temperature is a widespread *physical* barrier. The exclusion of "cold-blooded" animals, such as amphibians and reptiles, from the occupation of

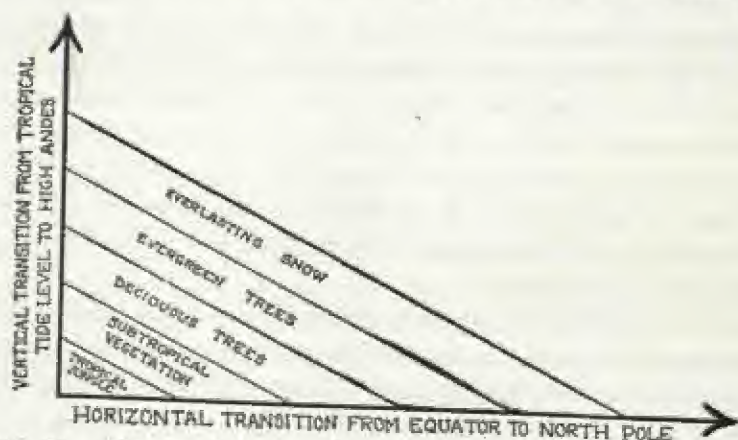


Fig. 78. Diagram of the general parallel sequence of organisms in altitude and longitude.

lands of prevalingly low temperatures, is quite evident. In general temperature zones extend not only in latitude north and south from the equator, but also in altitude in a parallel succession from tropical sea level to high mountain peaks (Fig. 78).

In the ocean, *pressure* acts as a barrier that stratifies the inhabitants within certain limits to which they have become specifically adapted. Deep-sea fishes cannot pass freely from abysses to surface waters, nor can pelagic

forms sink far below and survive. Similarly in the air there is an upper altitude limit beyond which flying birds cannot rise.

Humidity sets up a barrier which, according to its degree, is largely impassable to exploring organisms, dependent upon a certain optimum of moisture.

Light, another physical barrier, halts the traffic of nocturnal darkness lovers, although it usually has more of an ecological than chorological bearing. Green plants, on the other hand, do not live in the abyssal regions of the ocean because photosynthesis cannot be carried on there in the absence of light.

Geographical barriers are such features of the earth's surface as oceans, land masses, rivers, mountains, waterfalls, deserts, forests, and the like. A barrier to one organism, however, may be a highway to another. Thus, a desert would form an impassable barrier to a squirrel but not to a camel, while a forest in which a squirrel would revel would prove an effectual barrier to a camel.

Biological barriers are bound up in the first place with the eternal food problem, since absence of food of a particular kind in a region may prevent the advance of invading animals, while poverty of soil discourages occupation by plants dependent upon the missing soil constituents.

Secondly, biological barriers often take the form of other animals, by habit predaceous or parasitic, which hinder or forbid advance in certain directions.

Thirdly, the greatest biological barrier of all is man, since he is able to control the forces of nature far more than any of his animal allies. It should also be pointed out that limiting biological barriers may exist within animals themselves in the form of scanty wits, lack of initiative or adaptability, causing failure to enter into new areas even though the door of opportunity swings wide open.

If the factors of expansion and repression were equal in all directions, the area occupied by each species would remain constant as a perfect circle, but such a condition is unknown. The irregular shapes and boundaries of claims actually staked out in nature by various organisms proclaim the complex interaction of the fundamental opposing forces that determine distribution.

IX. CLASSIFICATION OF LIFE REALMS

An attempt has been made by chorologists to divide the land masses of the world into *life realms*, according to the distribution of animals and

mammals are warm-blooded, capable of occupying a great range of habitats, and being the most recently evolved large group of animals on the earth, have not had as much time as other types of animals to radiate from their centers of origin, with consequent confusion as to which species are native or endemic, and which introduced.

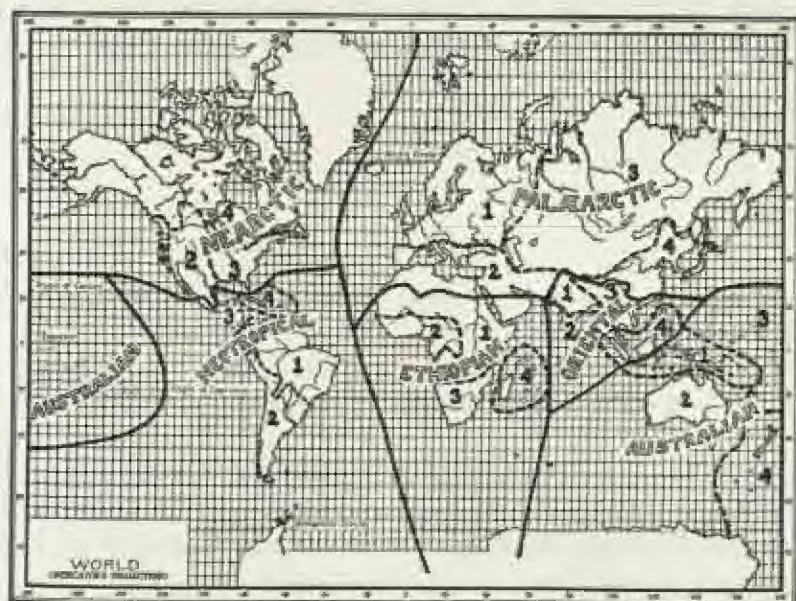


Fig. 79. Mercator map of the world, divided into zoological regions and sub-regions. Compare with Table I. (According to Wallace.)

Wallace's classification consists of six large regions, each divided into four subregions, as indicated in Table I. This table shows also the number of different *families of mammals* represented in each of the 24 subregions. It will be seen that bats (*Chiroptera*) are most generally represented, there being no subregion that does not have at least one of the five families of bats within its borders, while whales (*Cetacea*) do not appear at all, because they are not definitely associated with any land masses.

The richest subregion so far as numbers of mammalian families goes is the *South African*, although the *East African*, *West African*, *Mediterranean*, and *Indo-Chinese* are likewise conspicuously populous. The poorest is the *New Zealand* subregion that has no native mammals with the exception of two families of bats.

The mercator map of the world (Fig. 79) shows roughly the extent of each of Wallace's regions and subregions.

The study of chorology helps to solve such puzzles as (1) why related species, like the edentates in South America, are found in the same continental areas; (2) why areas physically alike, as Africa and South America, have different kinds of inhabitants; (3) why an original center for a species, like Wyoming for lemurs, may have no living representatives today; and (4) why regions near together, for example, Florida and the Bahamas, may have quite diverse faunas and floras, while regions remote from each other, like North America and Eurasia may have many similar forms.

The Distribution of Animals in Time— Palaeontology

1. VANISHING SPECIES

It is quite as essential to an intelligent understanding of living organisms upon the earth today, to have some vision of the long pageant of preliminary life in the past, as it is for a statesman to be well versed in the history of events leading up to the state of affairs with which his present problems are involved.

Species of animals and plants, like individuals, pass through successive stages that resemble the phases of a single life. Expanding childhood, vigorous youth, sustained maturity, and decrepit old age succeed each other only to end inevitably in death or extinction. Sometimes a species like an individual may complete its life without leaving any issue behind, but oftener, in the long course of its existence, it somehow gives rise to species different from itself, a process which has brought about the infinite diversity of living forms that connect *monad* with *man*.

Certain conservative kinds of organisms that are well adapted to their niches in nature persist, retaining their characteristics without significant evolutionary advance for unthinkably long periods of time, while other species, exhibiting a wider range of variability, live a faster, more diversified life and advance more rapidly along the transforming highway of evolution, only to meet extinction sooner. The brachiopods, *Lingula* and *Terebratula*, for example, the modern living representatives of which are hardly to be distinguished from remote fossil ancestors found buried in the most ancient sedimentary rocks, are instances of conservative species that have shown almost no progress, while trilobites, ammonites, pterosaurs, and dinosaurs are large representative groups of more ambitious animals, of astonishing diversity of form and structural detail, which have long since paid the death penalty for their high degree of specialization.

Examples of all stages of the process of coming to an end on the part of a species may be cited. For instance, among birds the ivory-billed woodpecker and California condor are probably marked for extinction in the near future. This is not so much because they are being crowded off the earth by dominant man as because they are in the biological blind alley of overspecialization with a consequent lack of ability to adapt themselves to changing conditions, which means that they are nearing the end of their organic resources. In fact, birds taken as a group are so highly specialized that they have no future evolutionary escape, since that is possible only in generalized types having capacity for further adaptation.

There are people now living who remember the hordes of passenger pigeons that formerly darkened the skies, but the last individual of this species died in captivity only a few years ago, while the passing of the dodo, the great auk, and Steller's sea cow are matters of recently recorded history. The hairy mammoth, New Zealand moa, sabre-toothed tiger, and woolly rhinoceros came to their end just before the beginnings of recorded human history. Back of these recent antiquities stretches a long interminable line of various species whose chapter of existence closed so long ago that our ordinary measures of time entirely fail to express the fact adequately.

There is no doubt that living species number but a small fraction as compared with vanished ones formerly peopling the globe, whose race has long since been run.

The dawn of life is unknown, for the oldest sedimentary rocks in which the first known evidences of life appear yield a wide variety of forms, such as protozoans, sponges, corals, jellyfishes, echinoderms, worms, brachiopods, mollusks, and trilobites. This means that the great Canterbury Pilgrimage of organisms had already been traveling for some time along the evolutionary road, before we catch our first glimpse of the pageant.

II. FOSSILS

Fossils are nature's hieroglyphics. They include the sum total of our actual documentary evidence of organic evolution, and besides form the alphabet in which the language of biological history is written. Sir Charles Lyell, the eminent geologist who did so much to influence young Charles Darwin at the beginning of his career, defines a fossil as "any body or traces of body, animal or vegetable, buried and preserved by natural causes." Every fossil is either ancestral to some living thing, or is representative of an extinct line.

The science of fossils, or the ancient history of animals and plants, is called *Palaeontology*.

1. Former Ideas About Fossils

Fossil remains of animals and plants, although known for a long time, have been variously misunderstood in the past. To Aristotle and the ancients they were artificial results of spontaneous combustion, or abortive attempts of inorganic matter to take on the form of life. Empedocles, who found fossil hippopotamus bones in Sicily, thought he had discovered a battle-ground where gods and titans fought. Henrion, in 1718, regarded fossils as molds and casts left over in the creation of animals and plants. He was the cock-sure writer who reported that the height of Adam was 123 feet and 9 inches, but since he carelessly neglected to specify whether or not the measurement was taken in his "stocking feet," and as he did not make clear how he arrived at his result, his opinion is regarded with some suspicion by modern science.

As late as 1823 William Buckland of Oxford wrote learnedly of fossils under the title, *On Observations on Organic Remains attesting the Action of a Universal Deluge*. Lyell states that it took a hundred and fifty years of dispute and argument to persuade scholars that fossils were really remains of what were once living organisms, and a hundred and fifty years more to convince them that they were not the results of Noah's flood.

Today a vast number of fossils have been recovered from oblivion from many parts of the world, and together they present a most illuminating and convincing mass of evidence concerning the ancient inhabitants of the earth. Even when fragmentary and imperfect, as most of them are, they furnish irrefutable proof of vanished life. The only questions that arise about fossils today concern the restoration of missing parts, the period or geological horizon when they lived, and their place in the evolutionary series. Dr. Lull of the Peabody Museum at Yale University, whose wide knowledge of fossils gives weight to his opinion, declares that "of the finally established facts which the fossils proclaim, we are as certain as we are of anything in this world."

2. Conditions of Fossilization

Various factors are involved in the process of fossilization. There is no reason to believe that these factors which have been effective in the past are not at work today. The great majority of individual animals and plants do not become fossils, but return at death to their inorganic origins along the route of decay, or by being devoured by animals.

It is usually essential that hard parts like bones, teeth, shells, scales, or chitin be present, and that the conditions for natural burial and the exclusion of air be such as to aid in the preservation of these parts.

However, Dr. C. D. Walcott has published a book of unexpected facts concerning *Fossil Medusae*, in which are pictured a great variety of these fragile creatures which succeeded in leaving a fossil record of themselves in spite of the fact that their jellylike bodies had no hard parts, and were over 95 per cent water.

The manner of burial in fossilization may be sudden and catastrophic, as by landslide, earthquake, devastating flood, overwhelming sand storm, or by a rain of volcanic ashes such as fossilized the entire cities of Herculaneum and Pompeii, or it may be exceedingly slow, as in the formation of sedimentary rock under water, the incrustations resulting from immersion in mineral-impregnated hot springs, or by the drip of limy water which forms stalactites and stalagmites in limestone caverns.

Quicksands, swamps, and bogs may engulf animals also and thus favor fossil formation by preventing rapid decay through the exclusion of air. As a matter of fact "bog water" is said to possess antiseptic properties to a remarkable degree.

Amber, which is fossilized pitch, or the solidified juice of resinous plants, furnishes another kind of burial place. Insects crawling on the trunks of ancient conifers, that became entangled in the sticky exudations there, have succeeded far better than any ancient mummified Egyptian, dreaming of immortality, in perpetuating their mortal bodies intact in a world of universal decay.

At Rancho la Brea, near Los Angeles, California, there are famous asphalt beds in which at some time long ago a great variety of animals, horses, tapirs, llamas, elephants, mastodons, giant sloths, huge wolves, lions, and sabre-toothed tigers, were not only entrapped and killed but were also preserved as fossils.

In detritus-filled caverns where dying animals have retreated, fossils are frequently found.

Sixty miles north of the Arctic Circle at Beresovka, in Siberia, a mammoth was discovered in a pit, frozen and so perfectly preserved in ice that some of the flesh was eaten by the discoverers, many thousand years after it was accidentally placed there in cold storage. This was not an isolated case. Many other instances of frozen carcasses of mammoths have been reported in northern Siberia.

On oceanic islands, such as the Chincha Islands off the coast of Peru, where for long periods of time sea birds have resorted to nest and where

there is scarcely any rainfall, the dried excreta of birds, commercially known as "guano," is deposited, frequently to a depth of several hundred feet, forming a natural burial place for organic remains.

In the Peabody Museum at Yale University is the skeleton of an extinct species of ground sloth, *Nototherium*, that was recovered from a cave in New Mexico where it was buried and preserved in bat guano. The preservation was so complete that it was possible to determine by the stomach contents that it died in the spring of the year, and that the vegetation of Pleistocene times was practically like that of today.

3. Uses of Fossils

Fossils, as Dr. Joseph Leidy many years ago quaintly said of the Protozoa, are chiefly useful as "food for the intellect."

Among various intellectual uses to which fossils are put, not the least is that of "faith testers," so called by good people alarmed at the silent evi-

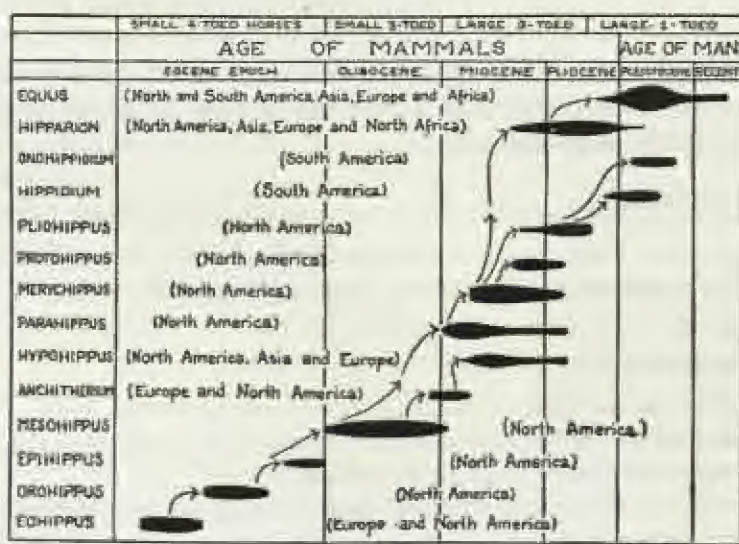


Fig. 80. The evolution of the modern horse, *Equus*. (After Matthew.)

dence thus presented of the great antiquity of the earth which they had been taught to believe had been created only a few thousand years ago. To the scientist these "medallions of creation" show first of all something of the racial history of animals and plants. In the absence of direct evidence, the past history of most animals and plants must remain largely a matter of conjecture, but there are some authentic instances of modern animals whose

ancestral modifications are written very legibly in the fossils that have been found. For example, the horse has a well established family tree extending backward without serious gaps for at least three million years to the little four-toed ancestor, *Eohippus*, of Eocene days. The actual fossil evidence for this remarkable pedigree may be seen by any visitor at the American Museum of Natural History in New York City, or at the Peabody Museum of Yale University in New Haven (Fig. 80).

Fossils are furthermore useful as *indicators of past climatic conditions* on the earth. The discovery of fossil palms in Wyoming, breadfruit in California; ferns in Greenland; reindeer in France; and musk oxen in Kentucky, records the indisputable fact that profound changes in climatic conditions have occurred in all of these places in the past.

Fossils also serve as *measures of geologic time*. Just as the date upon the corner stone indicates the year when the building was dedicated, so the presence of certain types of fossils in a particular stratum of sedimentary rock indicates the approximate time when those rocks were laid down. Or to state the value of a time measure by a further comparison, just as the character *f* instead of *s* on the page of an old book measures the limit of its publication by the year 1800, about which time the character *s* replaced *f* in general use, so the presence of a time-dating fossil on a geologic page measures the limits of its formation.

4. Kinds of Fossils

The following classification of different kinds of fossils is modified from that given by Professor R. M. Field in *Science* for June 25, 1920.

I. Those furnishing *direct* evidence:

1. *Actual remains*, such as insects in amber, and mammoths in ice;
2. *Minute replacements*, molecule by molecule of the original organic matter by mineral salts, resulting in *petrification*;
3. *Coarse replacements*, secondhand copies of originals by means of molds and casts;
4. *Prints and impressions*, of leaves, jellyfish, etc.

II. Those furnishing *indirect* evidence:

1. *Coprolites*, that is, solidified excreta or casts of the same;
2. *Artifacts*, such as ant-hills or prehistoric fashioned flints;
3. *Tracks, trails, and burrows*, all autographs of living animals;
4. *Geologic formations*, originating from organic sources, such as graphite, limestone, flint, coal, and petroleum.

III. IMPERFECTIONS IN THE RECORD

Huxley said that the whole geologic record of fossils is "only the skimmings of the pot of life." Although incomplete it is nevertheless the most convincing evidence of the story of the past.

The absence of suitable conditions for fossilization which surrounds the passing of the vast majority of animals and plants, as well as the inaccessibility to man of most of the fossils that actually succeed in being formed, make the task of the palaeontologist a particularly difficult one. The pages of the Great Stone Book on which the buried dead have written their own autographs cannot be freely shuffled over in order to read the story contained therein, because they are firmly stuck together. The fossil writing is, therefore, quite inaccessible except as lucky chance reveals enticing fragments of it, as when slow erosion bevels down the margin of the page exposing some few organic syllables, or when, by the puny engineering feats of man, the surface of the earth is somewhere scratched open, accidentally uncovering part of its buried treasures.

In many instances the natural sequence of rock stratification has been so confused that the student finds the pages of his book misplaced, by distortion, faulting, or folding, as in mountain formation. The more recent strata sometimes even come to lie beneath the older ones. The irregular and fragmentary character of the fossiliferous strata thus greatly increases the difficulties that confront the student who would correctly read the story of the past.

Sedimentary rocks of the earth's crust containing fossils are not arranged in uniform continuous strata that envelop the entire globe like the layers of an onion, but form in patches of unequal thickness and extent, according to the distribution of the water areas at the time of their deposition. There is no doubt that the earlier records of life in the form of fossils have in many cases been entirely obliterated by the action of heat and pressure during the metamorphosis of rocks into gneiss, marble, and granite, while the fossils that are buried in sedimentary rocks of the ocean floor are "forever hidden from hammer and mind."

According to the Bureau of Mines, Department of the Interior* the deepest hole that man has ever made down into the undisturbed fossil-bearing epidermis of the earth is in West Virginia, where borings to the depth of 7579 feet were made in search for natural gas. The deepest mine in the world is said to be the St. John del Rey mine in Brazil, while the "Village Deep" workings of the Transvaal gold mines of South Africa take

* *Science*, N. S., LX, No. 1541.

second rank with a depth of 6263 feet. In the United States the deepest mine workings are those of the "Calumet and Hecla" in Michigan which are reported to have reached 5990 feet below the surface. This is a distance of about a mile and is the nearest approach that man has ever made to the center of the earth. These extraordinary depths when compared with the total diameter of the earth, or even with the known thickness of fossiliferous rocks, are so insignificant that it is doubtful if they could be graphically represented to scale even by a shallow scratch on the surface of a four-foot globe. David Starr Jordan has truly said that the case of the palaeontologist is much like that of a traveler who, landing for five minutes on some remote corner of Australia, forthwith attempts a description of the entire continent from the observations made. The wonder is not that so little is known of the fossil record of animals and plants, but that, in the face of so many difficulties, so complete and connected a story of ancient life has been unearthed.

IV. A GEOLOGIC TIME SCALE

The fragment of eternity that comes within the vision of the geologist has been divided into unequal *eras* of time, beginning after the earth had cooled down enough to be clothed with an atmosphere and to have its surface diversified into areas of land and water. See Table II. The succeeding eras are measured by the time taken to form stratified rocks through the erosion and disintegration of the original fire-fused rocks, and the subsequent rearrangement of their component particles as sediment under water. Such sedimentary rocks afford sanctuary to organic remains and form the happy hunting grounds of palaeontologists.

Eras from ancient to modern times are: **ARCHAEOZOIC**, **PROTEROZOIC**, **PALAEZOIC**, **MESOZOIC**, and **CENOZOIC**.

The *Archaeozoic Era* is characterized principally by igneous and metamorphosed rocks without proved fossils, although traces of graphite indicate that plant life, probably in the form of primitive seaweeds, must have been in existence. The fiery furnace that fashioned the archaeozoic rocks, however, was no suitable place for the preservation of whatever organic remains existed in those formative days.

The *Proterozoic Era* saw the slow rise of the lower plants and most of the main general types of invertebrate animals. Together with the Archaeozoic Era, according to Professor Schuchert, it constitutes over one half of the total column of known sedimentary rocks, which reaches all together a maximum thickness of 114 miles in North America, although he qualifies this statement by saying: "In no one place, however, can be seen more than

a small part of this record, for usually the local thickness is under one mile, though there are limited regions where as much as twenty miles of it are present."

TABLE II. A Geologic Time Scale (After Schuchert and Dunbar)

ERA	PERIOD	TIME *	CHARACTERISTIC FEATURES
Cenozoic	Quaternary	1	Periodic glaciation. Evolving of man. Mammals evolve rapidly. Man diverges from apes.
	Tertiary	65	
Mesozoic	Cretaceous	200	First placentals. Extinction of dinosaurs, pterodactyls and toothed birds.
	Jurassic		Rise of teleosts, birds, and flying reptiles.
	Triassic		Rise of dinosaurs. First primitive mammals.
Palaeozoic	Permian	550	Rise of reptiles. Another great ice age.
	Carboniferous		Rapid evolution. Many extinctions.
			First known reptiles. Rise of insects.
			Accumulation of coal.
	Devonian		First known amphibians. Rise of fishes.
	Silurian		First known land flora.
Proterozoic	Ordovician	1050	First fishes (ostracoderms).
	Cambrian		Abundance of marine invertebrates.
Archaeozoic		2000	Origin of protoplasm and simplest life. Little evidence of life. No fossils.

* Millions of years estimated to have elapsed since beginning of era or period.

The *Palaeozoic Era* has been called the "Age of Fishes" because these animals became dominant during this time. The actual interval which elapsed in the *Palaeozoic Era* has been estimated as about 300 million years, surely sufficient time for many dynasties of plants and animals to have had their day.

Following the *Palaeozoic*, the *Mesozoic Era* witnessed the "Golden Age of Reptiles," some 150 million years long.

Finally, the *Cenozoic Era*, or "Age of Mammals," probably represents a little more than 60 million years. The geologists usually subdivide the *Cenozoic* into seven epochs so that beginning with the oldest, the Tertiary

is made up of the Paleocene, Eocene, Oligocene, Miocene and Pliocene which are then followed by the two Quarternary epochs, the Pleistocene and Recent. During the Pleistocene there were great climatic changes in northern Europe and North America. Possibly as many as four different times a gradual fall in the temperature of the northern United States and southern Canada resulted in a southward advance of the ice sheet to cover these areas for tens of thousands of years, only to be followed by a sufficient rise in temperature to bring about a retreat of the glaciers and return of these areas to temperate or even tropical conditions. Thus periods of glaciation alternated with interglacial periods. Similarly, areas of northern Europe were subjected alternately to long periods of glaciation and temperate climates.

The most recent episode in all this great moving spectacle of earth transformation is the story of *human evolution*, extending over only a few hundred thousand years at the outside, which in comparison with the stretches of time under consideration is but the thinnest surface film on the face of an abyssal ocean. Our actual fossil records of man are limited to Pleistocene and Recent times.

V. PICTET'S PALAEOONTOLOGICAL LAWS

A summary of some of the more important conclusions which follow from a study of fossils is embodied in the six "laws" adapted from *Traité élémentaire de palaeontologie* by Jules François Pictet (1809-1872), as follows:

- (1) All stratified rocks may contain fossils, therefore, *life has been present on the earth at least since the beginning of the Palaeozoic Era.*
- (2) The oldest strata contain extinct species and largely extinct genera, while more recent strata contain forms like the living, therefore, *the deeper the stratum the more divergent from those now living are the forms found therein.*
- (3) Different fossil faunas and floras follow each other in the same sequence everywhere, the layers nearest together stratigraphically contain forms most alike, therefore, *fossils show the evolution of forms from one another.*
- (4) Constant change is the inevitable law of life. Species characteristic of one level or time are partly or completely replaced later by other species, therefore, *species are not permanent or unchanging but are constantly giving way to modified forms that are presumably better qualified to occupy their place in nature.*

- (5) Species, as well as individuals, pass regularly through a cycle, including infancy, youth, maturity, and senility, therefore, *many groups of organisms* (as graptolites, trilobites, and ammonites), *have died out entirely and do not reappear, having completed their cycle.*
- (6) The approximate age of any stratum may be determined by the degree of similarity of its fossils to living forms. Similar fossils in different regions are indications of geologic strata of contemporaneous formation, therefore, *fossils serve to determine the age of rocks in which they are found.*

Man in the Making—Anthropology

I. THE ANCIENT HISTORY OF MAN

One of the riddles that perennially charms and challenges us, is the origin of mankind on this earth, for the farther back we go the more vague is our knowledge about man. As a matter of fact it would be much easier to collect data about the *iniquity* of man than about his *antiquity*, because then we would have no lack of material for our discourse.

The subject of the antiquity of man must always remain more or less shrouded in mystery. The reality of human antiquity, however, even in the absence of specific details, is beyond question.

Twenty years ago Professor Walter drew the following personal illustration. "The writer was born sometime in the nineteenth century. In the eyes of children of the twentieth century he must seem to be quite ancient. He can remember when there was not a single automobile in existence. He has lived through the entire Golden Age of the Bicycle and participated in its rise and fall. He recalls when there was no radio, no telephone, no phonograph, no electric lights, no X-rays, no typewriters, no motion pictures, and when *Darius Green and his Flying Machine*, by John T. Trowbridge, represented the final word in aviation. He remembers his grandparents as very old people, associated with ox teams and candlelight, for they were babes in arms when the war of 1812 was being fought. Their grandparents in turn lived before the Revolutionary War and even traditions about them are now vague and hazy. Back of them there must have been many other generations, but they lived so long ago that the present day has entirely lost sight of them." Beyond this personal survey, it is possible to resort to pages of history, going back in imagination to hoary landmarks of time such as the discovery of America, the Norman Invasion, the dramatic beginnings of the Christian Era, and far beyond these milestones to remote semi-mythical days when the Ten Thousand beat their famous retreat, or the Children of Israel passed dry-shod through the Red Sea, or when Tutankhamen was living flesh and blood instead of a celebrated mummy.

The palaeontologist laughs in his sleeve at anyone who pauses to consider such contemporary events as these, while the astronomer, dreaming of the majestic march of worlds other than ours, pities the short-sighted palaeontologist who is content to dwell on fragments of time as slight as Geologic Ages.

How far back into the shadowy past can the flickering torch of humanity be followed? What are the facts about the antiquity of man? Was there ever a time so remote that man was not man but something else? The sciences of *Anthropology*, and *Prehistoric Archaeology* are concerned with questions such as these. To confine ourselves to the events of our own day and generation, absorbing though they be, is like trying to breathe in a small, closed, stuffy room.

II. TRADITION AND EVIDENCE

Various traditions of human origins are a part of the folklore of every racial stock. One legend of the sudden inorganic origin of mankind is that of Deucalion and Pyrrha who, at the suggestion of Jupiter, peopled the earth by simply throwing stones over their shoulders, the stones becoming full-grown men and women according to which one of the celestial pair did the throwing. If these wonder-workers had operated upon a glacial hillside of New England, instead of the summit of Mount Parnassus where stones are rather scarce, no doubt the overpopulation problem would have become acute much earlier.

The Greek and Roman classics are full of naïve tales of dryads born of trees, and of Galateas coming to life from cold marble or lifeless ivory. Such stories and traditions, however, are in no sense *evidences* of the actual origin and antiquity of mankind on the earth. These evidences must be sought for in less romantic records of written history, in human fossils, and in persisting works of vanished hands, or indirect testimony of various kinds from other sources.

In America historical records of man practically date from the discovery by the whites only a few centuries ago, although there are abundant architectural remains in Mexico, Central America, and South America, that mark the presence of earlier, highly advanced civilizations, now vanished.

In Europe man was in a condition of illiterate savagery long after he had attained a high degree of development elsewhere. Recorded human history goes back with undoubted assurance only about 5000 years, continuing in Egypt and Mesopotamia with halting steps for perhaps 2000 years more;

after which the historical record fades, and it becomes necessary in tracing the antiquity of man to resort to the unwritten evidences of *prehistory*.

The prehistoric evidences of human antiquity may be grouped in five categories, as follows:

- (1) Indirect evidence from the length of time during which the earth has been habitable by man;
- (2) Indirect evidence from the amount of time which must have elapsed in order to allow mankind to reach his present degree of development;
- (3) Indirect evidence from telltale fragments of extinct animals found associated with human remains;
- (4) Direct evidence from actual prehistoric human bones;
- (5) Direct evidence from the enduring handiwork of man.

Some brief explanation and elaboration of these different lines of evidence is necessary to make their content clear.

III. THE HABITABLE EARTH

Astronomers, physicists, and geologists all testify to an unthinkable remote period of time since the stage has been set for human life upon the earth. It does not necessarily follow that man appeared as soon as the earth was ready for human occupancy, but this testimony definitely removes any objections on the score of possible geological unpreparedness with regard to his abiding place.

Scientists have made various estimates of the age of the earth, using for their calculations such yardsticks as the rate of radioactive transformations, the rate of heat loss from the cooling earth, the time required for the weathering of rocks and their subsequent deposition as sedimentary strata, or the time necessary to allow for the leaching out by water of the earth's crust enough to make the oceans as salty as they are today. The most recent estimates, based upon radioactivity, place the age of the earth at near 2000 million years. Hurst says: "One of the most remarkable features of modern science is the rapid expansion in recent years of the scientific estimates of the age of man, life, the earth, and the universe."

IV. THE TIME REQUIRED

Anatomically the human body is a collection of parts, assembled in varying degrees of perfection. There is every indication that the process of adaptation and modification is still going on, and that the human body as

we see it today is the result of repeated changes which have taken place in the past.

There is no structural detail in the human body not foreshadowed in the lower animals. The tracing out of resemblances and sequences in structure and organization between different animals and man is the peculiar province of *Comparative Anatomy*, and the mass of facts which constitutes the working basis of this biological science furnishes undeniable evidence bearing upon the antiquity of man. Just as a modern ocean liner, with its luxurious appointments and efficient intricate machinery, gives evidence of years of invention and experimentation with preliminary boats of a lesser order of elaboration, so the four-chambered heart, the larynx, or the brain of man, to anyone who knows something of the detail and complexity of these organs, tells a long story of preparatory variation and adaptation that must have required an enormous length of time for its accomplishment.

The science of *Chorology*, or the geographical distribution of animals and plants over the face of the earth, furnishes abundant evidence, of an undeniable kind, of the antiquity of man. The spread of human beings to the uttermost corners of the earth, which we recognize as an accomplished fact, could never have occurred by any series of migrations from common centers of origin without involving considerable lapses of time.

Two other fields of science, *Ethnology* and *Philology*, also prove the necessity of postulating an extended period of past time for the existence of man, in order to account for the present development of customs and languages.

Ethnology deals with the customs and institutions of the various *races of man*, while philology is concerned with human language and its evolution. In both of these fields man has attained a high degree of specialization. When one attempts to disentangle the various steps that must have preceded it, he is carried back so far that there can be no doubt about the antiquity of man. Moreover, as *Physical Anthropology* shows, the great race divisions of mankind into those dressed in integumental uniforms of black, brown, yellow, and white are of no recent growth but were already distinct long before the beginning of the historic period.

As for language which makes possible the oral transfer of experience, *Linguistic Palaeontology* shows that each of the branches of the so-called Aryan group of primitive languages, Persian, Indian, Semitic, Romance, Hellenic, Slavonic, Teutonic, and Keltic, has its roots buried in antiquity. The Hebrew and Arabic tongues are both ancient languages and neither the original of the other, and, therefore they are derived from still more remote ancestral sources.

V. ARCHAEOLOGICAL CHRONOMETERS

In some instances the handiwork of man has survived for a longer time than his own bones. The enduring touch of the vanished hand is particularly apparent in the case of the "indestructible flint" tools and weapons which he fashioned. The more important evidences of human antiquity that fall within the field of *Prehistoric Archaeology* are kitchen middens, pile dwellings, painted grottoes, monuments of various kinds, and fashioned flints.

1. Kitchen Middens

Kitchen middens are ancient garbage dumps where prehistoric man evidently congregated and feasted. Attention was first called to them by Thomsen in 1836 who described them from Denmark. Since then they have been noted in many other localities as widely separated as Japan, Spain, Brazil, Oregon, California, Maine, Denmark, the Aleutian Islands, Terra del Fuego, the north coast of Africa, and the shores of the Baltic Sea.

Kitchen middens consist principally of enormous masses of shells that could not have been collected together by any natural agency. They usually occur near the seashore, or where the seashore once was, because there primitive man had easy access to a natural food supply of shellfish. Mingled with shellfish remains are significant archaeological treasures of various kinds such as teeth, scales, bones of animals eaten, fragments of crude pottery, anvil stones, hammers, implements, and ornaments of different sorts made out of stone, obsidian, and flint, while pieces of charred wood and flat stones blackened with fire indicate, even to an amateur archaeological Sherlock Holmes, the use of fire by the people who left these extensive piles of refuse.

Some shell heaps, like those on the coast of Maine, for example, do not bear the earmarks of great antiquity, probably dating no further back than precolonial Indian days. Other kitchen middens, however, as those of the Baltic region, contain internal evidence of great age, for they consist largely of shells of salt-water mollusks, which cannot grow in brackish or fresh waters that characterize the Baltic Sea today, but must have flourished long ago when there was an open communication between the Baltic Sea and the salt ocean.

2. Pile Dwellings

The Greek historian Herodotus gives a detailed account of Thracian aborigines who dwelt in rude huts built upon piles out in the waters of Lake

Prasias in the land that is now modern Rumania. The most interesting exponents of this style of semi-aquatic architecture are the still older lake dwellers who lived and died probably some 6000 years B.C., or just beyond the outer halo of written history. They represent a primitive type of vanished civilization that came to flower particularly in the general region centering in Switzerland, where they erected their pile dwellings along the margins of numerous Alpine lakes. During a year of great drouth and low water in 1854, the submerged ruins of some of these curious pile dwellings came to light on the shores of Lake Zurich, and subsequently a large number of sunken remains of pile-built settlements have been discovered, while from the surrounding mud a great number and variety of relics have been recovered that make possible a fairly complete picture of the kind of life these ancient lake dwellers lived. The sites of over 200 of these prehistoric villages have now been located in the Swiss lakes alone.

The pile-dwellers represent a decided advance over the precarious nomadic life of the cave dwellers who preceded them. Building together upon piles out over the water enabled them to establish a haven of comparative safety from the assaults of hostile marauders and ferocious beasts, at the same time furnishing the security and leisure necessary in taking initial steps in invention, the arts of peace, and of organized warfare.

The pile dwellers made dugout canoes and crude pottery. Primitive agriculture and food storage were no doubt stimulated when pottery containers were invented. The ancestral fig-leaf had long since been replaced by furry skins and bark clothing on the part of the shivering cave dwellers of the icy Pleistocene times, but the pile dwellers went further and supplemented their wardrobes by fashioning coarse textiles, fragments of which were preserved buried in the mud. These may be seen in the *Antiquarisches Museum* in Zurich together with many other specimens of the prehistoric handiwork of the vanished race of lake dwellers. Living over the water doubtless insured some degree of primitive sanitation unknown, or at least unlikely, among those who pitched their camps in caves and forests on land. It cannot be doubted that the consequences following in the wake of ignorance of sanitation must have been quite as inevitable then as in these latter days when the bacteria of disease have been discovered and domesticated by modern man.

3. Painted Grottoes

About the time of the reindeer and wild horse occupation of what is now France and northern Spain, there flourished a remarkable period of prehistoric art, represented chiefly by crude drawings and paintings limned

upon the protected walls and ceilings of caverns. There have been catalogued from such troglodytic art galleries nearly 3000 different pictures in outline, monochrome and polychrome. In the Dordogne region of France, one single cavern, the "Combarelles," is a veritable prehistoric Louvre, which contains 109 wall pictures covering an area of over 2000 square feet.

The pictures are mostly outlines of animals, such as bison, reindeer, mammoths, wild horses, woolly rhinoceroses, and others, that were contemporary in Europe with the cave-dwelling, flint-using folk who drew them. Usually they are well enough done to be unmistakable. The most ancient of them, apparently the work of the Aurignacian wild horse hunters, are bare outlines roughly engraved on the cavern walls by means of flint tools, and probably by the light of flickering torches.

The best of these old animal pictures, as well as the majority of them, were evidently made later by the Cro-Magnon reindeer-hunting people, and are for the most part flat surfaces chipped into the solid rock and colored with various substances such as chalk, charcoal, red and yellow ochre, and other mineral pigments. The famous polychrome frescoes of the Altamira caverns in northwest Spain near Santander, which would be a credit to artists of a much later time, mark the highest point of excellence in glyptic art.

It is quite likely that the painted grottoes were not decorated as an expression of "art for art's sake," but as part of a magic ritual to aid the hunters in successful pursuit of their prey. Since the grotto artists or necromancers drew what they saw, a study of

their pictures throws considerable light upon the state of affairs in their part of the world some 15,000 to 30,000 years ago. As a single example, the skyline of the hairy mammoth is represented with a depression in the neck region (Fig. 81) which is absent from all modern proboscideans and is not evident on the fossil mammoth skeletons that have been assembled. This means that the living mammoth had a fat lump, not to be seen in the skeleton, posterior to the notch of the neck. The fat lump indicates storage of food which enabled these great beasts to live through

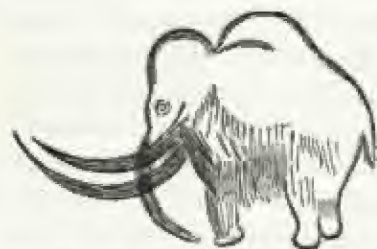


Fig. 81. A prehistoric sketch from a cavern in Dordogne, France, showing a hairy mammoth with a hump of stored fat on its back, suggesting that it lived in an arctic climate.

seasons of scarcity. The outline of the hairy mammoth as depicted by the Cro-Magnon artists in this way informs us that the painted grottoes were decorated when France had an arctic climate.

The approximate age of the painted grottoes is also determined in part by the kind of bones and flint implements found in the rubbish that filled the caverns, thus protecting the pictures throughout thousands of years from exposure and destruction. Certain other time marks, such as paintings of different ages superimposed one above the other, tell the story of different hands that wrought them. All in all these early attempts at artistic expression are direct evidences of the great antiquity of man, for of all creatures only man could have left such signs of the times.

4. Large Stone Monuments

The ancient Egyptians who built pyramids, sphinxes, and obelisks in the attempt to outwit the devastating tooth of time, were not the first to leave some enduring memorial of themselves to succeeding generations. Prehistory, as well as written history, bears witness to the same human desire for impressing posterity. This desire has found expression not only in the form of mounds or earthworks of unmistakable human workmanship, but also of large stones, or *megaliths*, arranged and set up in various unnatural ways.



Fig. 82. Megaliths of Stonehenge. (After Quennell.)

Large columnar stones set up on end are called *menhirs*. Of these over 700 have been located in Brittany alone. Primitive man must have exercised a good deal of engineering skill, probably by digging pits, building temporary inclined planes, and using pulleys of some sort, in order to jockey these huge stones into position. Their size and shape preclude the possibility of their placement by any natural agency.

Frequently menhirs were set up in parallel rows, termed *alignments*, or in circular arrangement, designated as *cromlechs*. A flat stone resting upon two uprights is called a *trilith*, but when several uprights support a top stone, like a rude table or altar, the structure is called a *dolmen*. Nearly

5000 dolmens have been found in France, while at Stonehenge and Avebury (Fig. 82) in England there are two very famous and much described collections of megaliths, arranged as alignments, cromlechs, dolmens, and single menhirs. The collection of megaliths at Avebury is more extensive than that at Stonehenge, but it is not as well preserved because many of the stones were removed to build the modern village of Avebury by people not interested in antiquities.

One cromlech 1200 feet in diameter, and made up of 100 separate stones each seventeen to twenty feet high, forms a part of the Avebury collection.

Some of the most curious and mysterious evidences of ancient human activities are the stone images of Easter Island. On this isolated island in the south Pacific, 2000 miles west of South America, there are over 600 stone statues, hewn out of volcanic tufa and weighing up to thirty tons each. They are all patterned alike, regardless of size, and represent a half-length human figure with hands placed across the front of the body. Most of the statues when discovered were found overthrown and the present scanty inhabitants of Easter Island have no traditions concerning how the statues came to be there. Their origin is one of the most puzzling of archaeological enigmas.

In addition to megalithic witnesses of the distant past there are *mounds*, *tumuli*, and *earthworks* of various sorts, that tell the same story of the antiquity of man. Some of these structures were no doubt connected with ancient burial customs or religious ceremonies, while others were probably once places of refuge, or fortresses, the ruins of which remain to remind us of the gray days during which our distant ancestors kept alive on the earth the precious spark of humanity.

5. Tools and Weapons

Man, of all animals, is the only one fitted to grasp tools and weapons. The tools and weapons of other animals, such as horns, teeth, tails, claws, and hoofs, are a part of the permanent equipment of their possessors, built into the body, and may be improved or substituted for other tools only in the slow age-long workshop of adaptive evolution. After all it is the brain that makes the grasping of tools or weapons effective. Apes pound a stone with a nut, but man discovered that he got better results if he pounded the nut with a stone.

Some of the earliest tools and implements fashioned by man furnish direct evidence of human antiquity that antedates his oldest fossil remains. This kind of evidence is far more accurate and reliable than any historical chronicle whatsoever that has been colored by human judgment on the

part of the historian. Sir W. R. Wilde has emphasized this point by saying, "Men are liars, stones are not."

The materials employed in outfitting the grasping hand of man have been principally flint, which is composed of the finely crystallized remains of silicious sponges and other marine organisms, dissolved and redeposited in the form of irregular lumps. Quartz, and obsidian or "volcanic glass," which like flint fractures in flakes from cores by pressure or by percussion, were also employed, as well as horn, bone, shells, ivory, wood, and later on, metals. Of these various materials wood is the least enduring and so furnishes very little evidence today of the uses to which in all probability it was formerly put by prehistoric man.

Of the metals, copper occurs in comparatively free form in nature and was the first metal utilized by man. Malleable bronze, which is an alloy of copper and tin, was discovered or invented long before iron, "the great lever of civilization," was successfully smelted from the ore, beginning probably about 1300 B.C., on the shores of the Black Sea.

Archaeologists speak of successive stages of human culture based upon the materials employed in the manufacture of tools and weapons. They are the *Stone Age*, *Bronze Age*, *Copper Age*, and *Iron Age*. To them might be added a fifth, the *Steel Age*, in which we live today.

These ages are not uniform in origin or duration in different parts of the world. Egypt, for example, had already reached a high point in the Bronze Age at the time when Europe still lingered in the Stone Age of culture (Fig. 23), while in North America and Australia the Stone Age was in full swing when these countries were discovered by white men in recent historical times. Some races of man still living today, that have been isolated from contact with other races, such as the Hottentots of Africa, Veddahs of Ceylon, Botacudos of Brazil, Andaman Islanders, Fuegians, and Eskimos, are still in a very primitive stage of tool culture.

The Stone Age, before iron was applied to the follies of war or the arts of peace, offers a most fascinating field for study, since it furnishes the earliest direct evidence of human activity upon the earth. It is a field that has attracted many scholars. As late as 1938 there was opened in the Ohio State Museum at Columbus, a "Lithic Laboratory" in which to specialize in types of stone tools, showing the materials used, and the technics employed in making them.

The stone instruments of primitive man were fitted to a variety of uses. They include arrow-points, lance-heads, knives, axes, hammers, saws, choppers, borers, etchers, scrapers, punches, polishers, spark-producers, and ornaments. Their evolution tells the story of human progress through many cen-

TEN THOUSAND YEARS B.C.

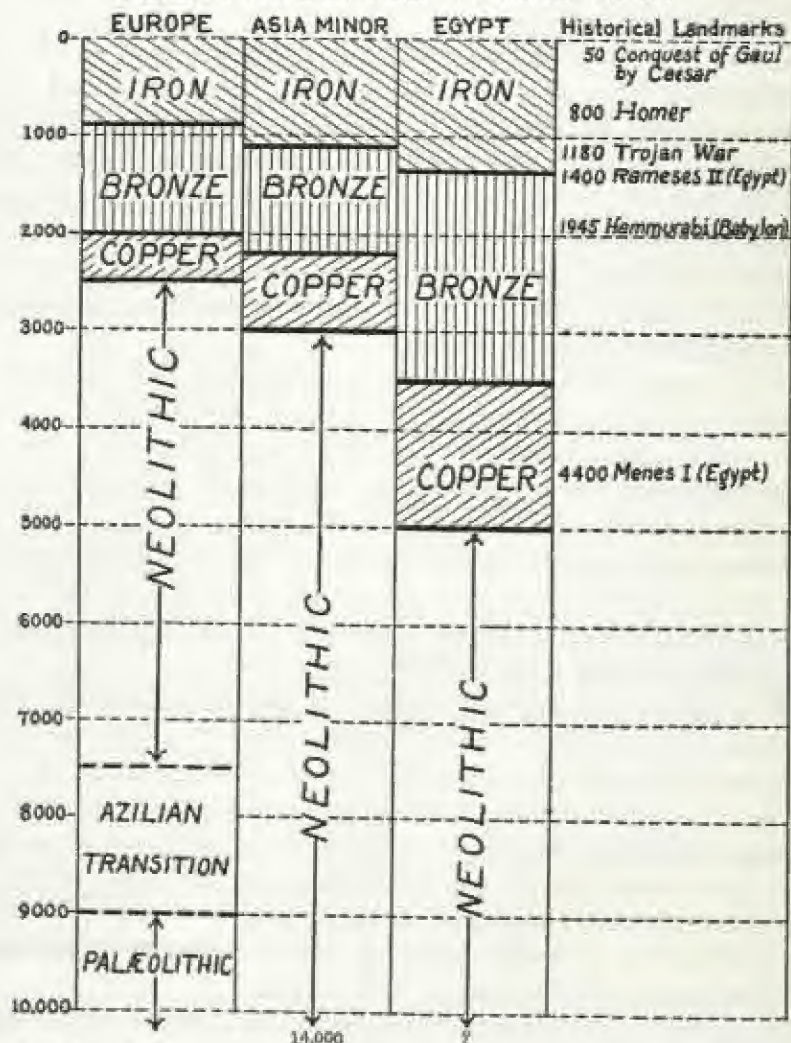


Fig. 83. A chart to show that "cultural ages," while following the same sequence in different regions, were not of equal duration. (Modified from Boule.)

tures of time. The interpretation and significance of this story got its initial start when M. Boucher de Perthes in 1838 discovered the first known authentic flint hatchet in a sand bed near Abbeville, France, together with rhinoceros and mammoth bones. Since then in the last century a very great number of flint tools and implements of different degrees of perfection in workmanship have been found and carefully studied. France has been

particularly fortunate, not only in unearthing these records of early man, but also in having distinguished scholars who have collected and described them.

According to prescientific interpretations the relics of the Stone Age, chiefly flints, were described variously under the name of "fairy darts" and "thunderbolts," and their origin assigned to the Druids, Romans, or the Devil, a convenient trinity which has been made responsible for other strange things as well.

Wherever fashioned flints have been found, even in such diverse regions as the Nile Valley, Algeria, Europe, England, Somaliland, and America, they exhibit the same universal sequence of patterns, and a parallel succession of evolutionary differences or degrees of refinement. It is thus possible to subdivide the Stone Age into four unequal successive divisions of workmanship, representing stages of human culture, namely, EOLITHIC, PALAEO-LITHIC, MESOLITHIC, and NEOLITHIC. See Figure 84. Experts have further arranged the successive cultures of the Stone Age into *subdivisions*, the names of which for the most part are derived from localities in France near which the typical characteristic flints were first discovered.

Reading downward from the most ancient to the most recent, they are as follows:

I. Eolithic Period

II. Palaeolithic Period

A. Lower Palaeolithic

1. Abbevillian (Chellean)
2. Acheulian
3. Mousterian



Fig. 84. Flints, representing three periods of the Stone Age. (Drawn from specimens in the collection at Brown University.)

B. Upper Palaeolithic

1. Aurignacian
2. Solutréan
3. Magdalenian

III. *Mesolithic Period*

1. Azilian
2. Tardenoisian

IV. *Neolithic Period*

Stone implements of the oldest type, representing the colithic culture, are termed *coliths* (Fig. 84). They mark the "great extent of time that has elapsed between the picking up of the first stones with an intelligent purpose, and the acquirement of sufficient knowledge to shape them into the crudest form of palaeoliths" (Wilder). Coliths, nowhere abundant, are always more or less problematical objects, since they are not undeniable artifacts in the sense of purposeful manufacture, but are merely pieces of stone of convenient size and shape to fit the hand and lend persuasive weight to the fist. They are distinguishable *by showing the effects of use*. The uncertainty connected with them depends upon whether they were bruised and fashioned by man or nature. Professor G. F. Scott-Elliot says of them, "Surely if there is little to prove that coliths were made by man, there is even less to convince us that they were formed in any other way."

The flints of the Palaeolithic Period, as contrasted with coliths that were perhaps accidentally scarred, are unmistakably the result of human manipulation. They are all definitely chipped and fashioned (Fig. 84), exhibiting an evolution of workmanship from crude lower palaeolithic forms, imperfectly worked, to exquisitely fashioned tools and weapons of later time in the "golden age" of the grotto painters.

The *Abbevillian* flints are almost exclusively the cores of nodules rather than flakes or fragments that have been chipped off. These flints are mostly oval hand-axes ("coup-de-poing" of the French), coarsely chipped. The idea of fastening the ax to any sort of a handle was yet to come.

Characteristic *Acheulian* tools were hand-axes more carefully sharpened and with straighter cutting edges than those of the Abbevillian. In both of these cultures hearths are occasionally found, indicating the use of fire by these early Palaeolithic men.

The flints of the *Mousterian*, chipped on one side only, were of considerably better workmanship than anything that had gone before. For

example, flakes from stone nodules were used as scrapers, knives, and with notched edges as saws, while the cores of the nodules were made into crude fist-axes.

The three subdivisions just enumerated make up the *Lower Palaeolithic Group*, as contrasted with the three following subdivisions, or *Upper Palaeolithic Group*, which brought in a "new kit of tools," showing the highest development of flint work.

The *Aurignacians*, preceding the Cro-Magnons, lasted some 7000 to 8000 years in Europe, and added bone and ivory harpoons to their equipment. Among other things they also invented needles, or slender splinters of bone with a hole in one end so that thongs of sinew could be threaded through and skins sewed together by means of them. One of the greatest of human inventions is the needle. No animal, even an ape with busy exploring fingers, ever conceived such an idea, much less put it into effect.

The most beautifully chipped of all flints are the thin "laurel-leaf" lance-heads of the *Solutréan* culture. From this time on the art of fashioning flints declined.

The *Magdalenian* subdivision is characterized more by the use of bone, horn, and ivory, and by polychrome paintings in caverns.

The *Azilian* and *Tardenoisian* subdivisions of the transitional Mesolithic Period, which followed the last glaciation, witnessed a further decline of the art of working flint, although it is apparent that handles were employed for ax-heads and arrow- or spear-points were bound by thongs to wooden shafts at that period. These two latter subdivisions are distinguished from each other by the fact that the *Tardenoisian* subdivision was characterized by the occurrence of *painted pebbles* of unknown use, not present in the *Azilian* culture.

The comparatively short *Neolithic Period* is distinguished from the Palaeolithic subdivisions not only because neolithic tools and weapons were fashioned into a larger variety of definite shapes for obvious uses, but also for the reason that they were *polished smooth* (Fig. 84). All evidence thus far gained shows that flints were chipped for thousands of years before man learned to polish them. The most important features of this period are, however, the beginning of the manufacture of pottery and the development of agriculture and domestication of animals.

Many flint instruments, particularly those of the neolithic type, continued to be manufactured and used long after metals were employed in the Bronze and Iron Ages, just as modern means of locomotion, such as ox-carts, horses, bicycles, automobiles, and airplanes, while tending to supersede what has gone before, still persist long after they have lost their dominance.

VI. HUMAN FOSSILS

The actual bones of prehistoric man furnish the best direct evidence of human antiquity, but unfortunately they are very scarce. This is due in part to the arboreal life of human ancestors whose dead bodies, left without burial, were liable to be devoured on the spot or subjected to immediate decay and disintegration.

Moreover, a large part of the earth, including many localities where human remains might have been overwhelmed and fossilized, has not as yet been thoroughly explored by competent scientists. Evidence of human antiquity from fossils has been acquired only within the last century. As late as 1852 the eminent French palaeontologist Cuvier, gave the famous opinion, backed by his extensive knowledge of what was known in his day, "*L'homme fossile n'existe pas.*" All the supposed discoveries of prehistoric human remains up to that time were shown to be of comparatively recent origin or not human at all. One often cited case is that of Scheuchzer, who found and described in 1732 what he called a fossil man, to which he gave the name *Homo diluvii testis*, or "man, witness of the flood," with the pious comment, "Rare relic of the accursed race of the primitive world. Melancholy sinner preserved to convert the hearts of modern reprobates!" This famous specimen, which now reposes in a museum in Haarlem, turned out, however, to be not a human skeleton at all but the bones of a giant salamander.

1. Java "Ape-Man"

Pleistocene deposits have yielded not only tools and weapons but many human fossils, the oldest of which bear resemblances to the early Pleistocene and Pliocene apes. Klaatsch, who speaks from a profound knowledge of comparative anatomy, describes apes as "unsuccessful attempts to compass the road to mankind from prehuman stock."

The German zoologist Haeckel was so confident that species intermediate between apes and man once lived that in 1866, before many discoveries of human fossils had been made, he assigned the tentative name of *Pithecanthropus* (ape-man) to the unknown, and prophesied its future discovery.

In 1891, however, Dubois, then an officer in the Dutch army stationed in Java, found fossil remains after extended search on one of the banks of the Solo River near Trinil, thus fulfilling Haeckel's prophecy. These remains were a skullcap, or *calvarium*, and a molar tooth, to which were added from the same locality later a left thigh bone and two other teeth, together

with a fragment of a lower jaw. These fragments of the "ape-man" were recovered some twenty yards apart, making the likelihood of intrusive burial improbable and casting doubt on the probability that the several bones did come from one individual.

Companion bones of various animals were unearthed that filled 400 packing cases. This material was brought back to Holland and subjected to painstaking study. The specimens included bones of the extinct proboscidian, *Stenodon*; the ungulates *Leptobos* and *Hippopotamus*; and the giant pangolin, species no longer inhabitants of that part of the world, as well as tapirs now found only in South America on the other side of the globe. Altogether 24 species of Pleistocene animals under 45 feet of undisturbed stratified deposits have been identified among these remains, fixing the time when *Pithecanthropus* lived as approximately 500,000 years ago (Fig. 85).

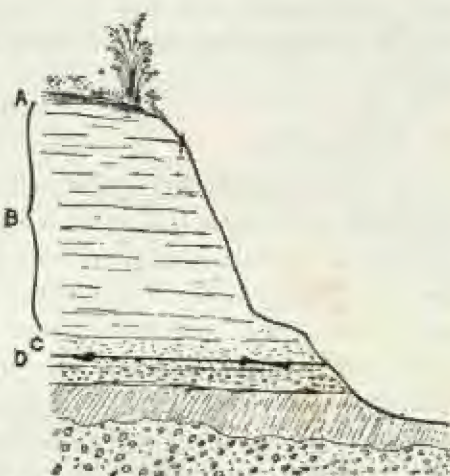


Fig. 85. Diagrammatic cross section through the fossiliferous strata in Java where the *Pithecanthropus* bones were found. A, surface soil; B, undisturbed sandstone; C, volcanic layer; D, level of the *Pithecanthropus* bones and of various extinct Tertiary animals. (After Dubois.)

Despite attempts of others to obtain additional specimens of the Java "ape man," none was found until von Koenigswald, between 1936 and 1939, unearthed portions of three

skulls and a lower jaw, also in the Solo River valley but near Sangiran, above Trinil. From the combined evidence of all available material it has been determined that *Pithecanthropus* had a somewhat apelike brain case with low forehead and heavy supraorbital ridges but with a capacity of slightly more than 900 cubic centimeters (Fig. 86). The brain would therefore be intermediate in size between that of the great apes, which ordinarily do not exceed 600 cubic centimeters, and modern man whose cranial capacity varies



Fig. 86. A comparison of the skull capacities of various primates. (After Boule.)

between 1200 and 1500. Although no tools have been discovered with any of the skeletal remains, primitive stone instruments have been found in Java in the same strata as those to which the specimens of ape man belonged.

From all of the evidence now available it is clear that *Pithecanthropus* was an erect-walking primate with the ability to use tools, and with features of the skull and brain which are more human than simian. He may have been a stage in the evolution of man or of at least a portion of the human race. As he apparently had European contemporaries it is quite possible that he represents but one branch of a human stock which had originated earlier.

2. Peking Man

At Choukoutien, some thirty miles southwest of Peiping, China, the investigation of a group of caves revealed middle Pleistocene deposits which included a number of skeletal remains of various animals. Dr. Davidson Black, of Peking Union Medical College, becoming interested in two teeth which were found, supervised further excavations which uncovered a third tooth, a lower molar, in 1927. He was so certain that the new find came from a primitive man that he established the new genus *Sinanthropus* for it. That he was justified was shown by the discovery, in 1929, of an almost complete brain case embedded in limestone under 110 feet of cave deposits. After Black's death, Dr. Franz Weidenreich continued the work and by 1938 nearly 40 *Sinanthropus* individuals were represented in the collection of teeth, jaw fragments, portions of skulls and a few parts of the appendicular skeleton.

Sinanthropus resembled *Pithecanthropus* in such features as a receding chin, large supraorbital ridges, and low forehead, but had a somewhat larger cranial capacity, the average of the capacities reported being 1075 cubic centimeters. Several other details indicate that Java man was slightly more primitive than Peking man who may have been an intermediate stage between Java man and Neanderthal man.

With the skeletal remains there have been discovered palaeolithic tools and hearths, good evidence that Peking man was a fire-user. As all of the skulls had the bases smashed in, it is believed that he was a cannibal who ate the brains and probably other parts of the body, even as *Homo* of recent years has been wont to do.

3. Heidelberg Man

The "Heidelberg man," *Homo heidelbergensis*, lived among animals that characterized the first interglacial period of perhaps 450,000 years ago. He was therefore an European contemporary of *Pithecanthropus*. This race is represented only by a lower jaw (Fig. 87), found in 1907 buried in a gravel pit near the mouth of the Neckar River valley about six miles from

Heidelberg, Germany. Over eighty feet of undisturbed sand and sedimentary rock had been deposited over this interesting ancestor. For subsequent centuries the slow eroding action of the Neckar river carved out the valley, before this famous human fragment was eventually exposed to modern view (Fig. 88).

The jaw is heavy, massive, and chinless. It is apelike in character but the teeth are comparatively small and have the shortened roots and dilated crowns that distinguish human teeth. With our knowledge limited to these interesting features of the lower jaw it is difficult to tell what may have been Heidelberg man's position with relation to other fossil men.



Fig. 87. Outline of the Heidelberg jaw, contrasted with that of the chimpanzee and man. (After Boule.)

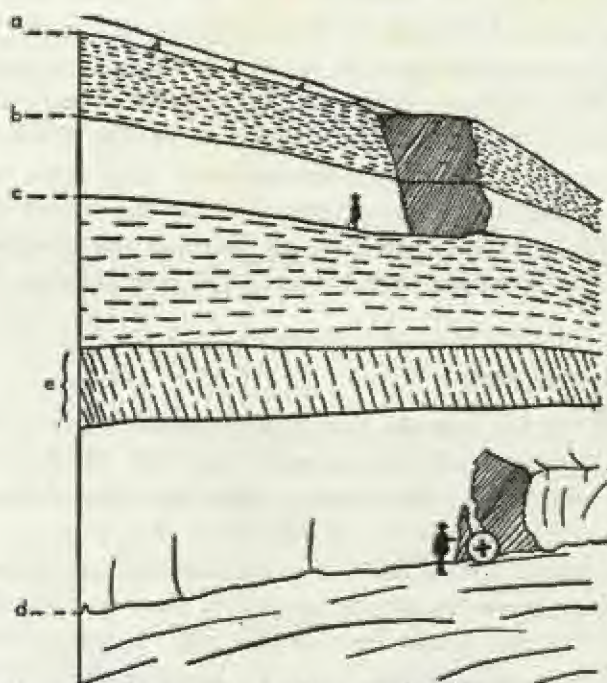


Fig. 88. Diagram of the sand pit where the Heidelberg jaw was discovered, a-b, layer of "Newer Loess"; b-d, "Older Loess"; c-d, Mauer sands; e, clay. The cross indicates the spot under seventy-nine feet of undisturbed strata where the fossil jaw was found. (After Schoetensack, in Osborn, *Men of the Old Stone Age*. Charles Scribner's Sons.)

4. Piltdown Man

Skull fragments, found by Charles Dawson in 1908 and 1911 near Piltdown Common, Sussex, England, so interested Sir Arthur Smith-Woodward

that he joined in the search for human fossils in that area. In 1912 these workers discovered a larger piece of a skull, and in 1915, about two miles from the first discoveries, part of a second skull. To this type of primitive man Smith-Woodward gave the name *Eoanthropus dawsoni* ("Dawson's dawn-man"). Early Pleistocene animal skeletons found in these same Piltown gravel beds show that this man was probably a first interglacial contemporary of Heidelberg and *Pithecanthropus*.

The lower jaw of *Eoanthropus* is almost completely apelike but the brain case is of a quite advanced type. The supraorbital ridges are reduced, the forehead high, and the cranial capacity near 1350 cubic centimeters. Except for the fact that the bones are about twice as thick as those of modern man, in this respect resembling *Pithecanthropus*, the brain case is quite modern.

Further evidence of primitive man in England was discovered by A. T. Marston in 1935 and 1936 at Swanscombe in the lower Thames valley. In the same stratum with Acheulian implements and middle Pleistocene fauna an occipital bone and then a parietal bone were uncovered. They closely resemble corresponding parts of the Piltown skulls and indicate a cranial capacity of somewhat over 1300 cubic centimeters but apparently belong to a later period, probably the second interglacial. Sir Arthur Keith, who has been cited as "perhaps the greatest authority on fossil man," believes these parts belonged to a later member of the Piltown group.

5. Neanderthal Man

In 1856, not far from the time that Darwin's *Origin of Species* (1859) appeared, throwing both the scientific and the theological worlds into intellectual convulsions, there came to light the original *Neanderthal man*, the first primitive fossil man to be discovered. This is an incomplete human skeleton unearthed by workmen in a detritus-filled cavern near Düsseldorf, Germany, high up on the precipitous side of a ravine about 60 feet above a stream and 100 feet below the top of a cliff. Together with the skeleton were found, embedded in hard loam, the bones of animals long extinct, the cave bear, woolly rhinoceros, mammoth, cave hyena, and other Arctic forms. Man is known by the company he keeps, and these bones with superimposed detritus covered over by undisturbed strata of sedimentary rock, put the seal of unquestionable antiquity upon the Neanderthaler.

The bones themselves, which have undergone more expert scrutiny than perhaps any other set of bones, indicate a burly, squat, bow-legged individual, with thick skull, projecting brows, low retreating forehead, and

receding chin, characters distinctly unlike those of modern man. That this individual was not a unique prehistoric hermit has been unquestionably demonstrated by subsequent discoveries in various localities in Europe, as well as in Palestine, of about 70 individuals represented by bony fragments of one kind or another, all agreeing essentially with the original find. The existence of this species of human beings, *Homo neanderthalensis*, whom the late G. Elliot Smith refers to as "weird caricatures of mankind roaming far and wide to satisfy their appetites and avoid extinction," is now no more in doubt than the existence of ancient Egyptians.

Accompanying Mousterian implements and Arctic, or glacial-period, animals indicate that the Neanderthals flourished between 150,000 and 115,000 years ago during the difficult last days of the great Pleistocene period. By the latter part of the fourth glaciation, 50,000 to 70,000 years

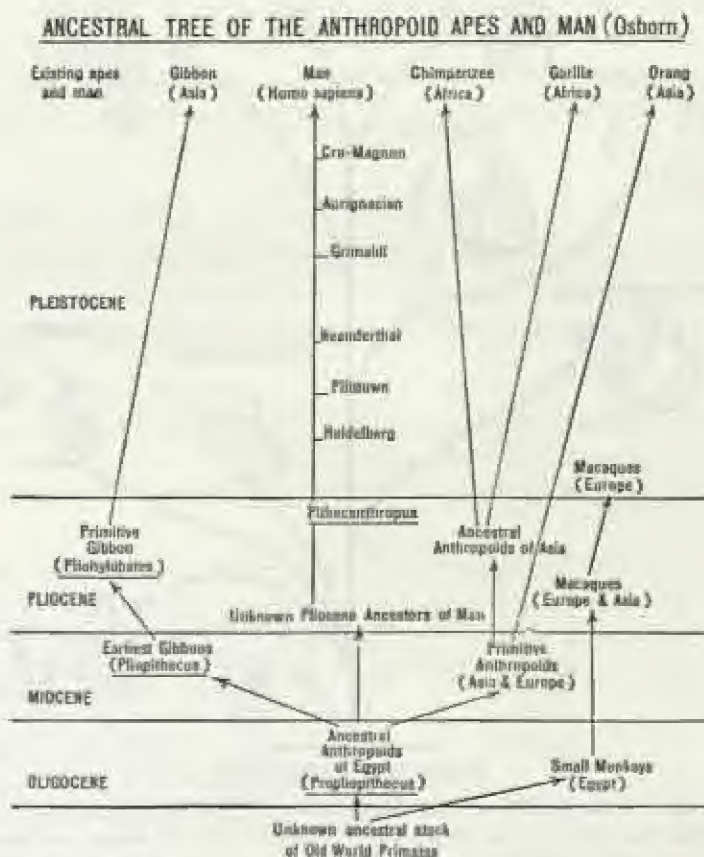


Fig. 89. Ancestral tree of the anthropoid apes and man, according to the conclusions of Osborn.

ago, they had disappeared and the caves were being occupied by men of our own species.

6. Cro-Magnon Man

The fossils thus far considered are conceded to be evidently human, although of species different from our own, *Homo sapiens*. There is considerable evidence that the men of modern types who superseded the Neanderthals were probably not their descendants but invaders from other regions, who had progressed to the modern type while Neanderthals had

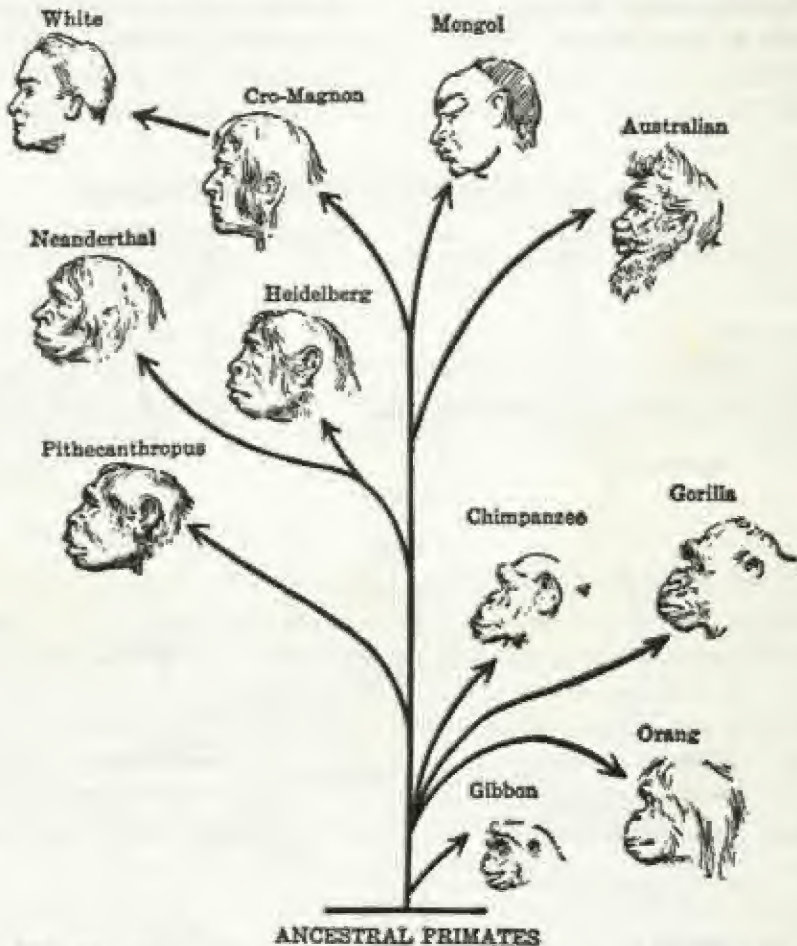


Fig. 90. Phylogenetic tree of the anthropoid apes, primitive man, and modern man, illustrated by drawings of heads some of which are reconstructed. (From Hegner, *College Zoology*, copyright 1942, by permission of The Macmillan Company, publishers. Drawings of the heads courtesy Amer. Mus. Nat. Hist.)

remained as "palaeontological hang-overs, outmoded survivors of an earlier stage of human evolution," to use the words of Professor E. A. Hooton.

One of the finest races physically that ever existed, of which many fossils have been recovered, was the Cro-Magnon race of reindeer hunters that lived 15,000 to 30,000 years ago near the close of the last ice age. These nomads of frigid days not only left some of their bones behind, that showed them to be tall finely built specimens of humanity with large capacious skulls, but they also left mural pictures of contemporary animals which they painted on the walls of their caverns. The bones of wild horses, wild boars, and reindeer, abundant all over that part of Europe where most of the fossil remains of man have been found, are eloquent witnesses of an ancient regime when man lived in a different world than that of today. In southern France alone there were eighteen species of large animals which were formerly common that have now migrated to more congenial climes. Of these, thirteen, like the reindeer, have gone north, and five, like the chamois and mountain goat, have retreated to cool mountain tops.

Figures 89 and 90 are attempts to indicate the probable relationship of the better known primates.

VII. TIME SCALES

There is no doubt that, to our myopic vision at least, contemporary events of our individual lifetimes are the most interesting part of all human history, but a single lifetime of even "three score years and ten" is only one

TABLE III. Time Scale

(Based on the unit in which a human lifetime of "three score years and ten" is equal to one minute.)

	<i>Minutes ago</i>	<i>Hours ago</i>	<i>Days ago</i>	<i>Years ago</i>
A single lifetime	1			70
Columbus discovered America	6.5			456
Christian Era began	27.8			1948
Written history began	100	1½		7000
Cro-Magnon race lived	430	7		30,000
Neanderthal race lived	1000	16½		70,000
Pittdown race and Pithecanthropus lived	7150	119	5	500,000
Cenozoic Era began		15,476	645	65,000,000
Mesozoic Era began		47,619	1984	200,000,000
Palaeozoic Era began		130,952	5456	550,000,000

one-hundredth of the approximate time involved in written history. Historical events that seem very ancient in contrast to the times in which we now live, appear quite recent against the background of the "Cultural Ages" of the archaeologist, while in turn the cultural ages crowd magically forward into what seems like the immediate present when their position in geologic time is considered. It is a good thing occasionally to ignore the fleeting news events of the day and to stretch one's sense of time by probing into the abysmal past. Man is the only animal who has the capacity to look both ways and to be aware of the past and future.

Table III is an attempt to visualize the reaches of past time.

VIII. CONCLUSIONS

The continuing wonder of mankind is man. His achievements are like a rapidly widening wedge, awakening "undiminished interest in every man born into the world" (Huxley). The fascinating theme of the anthropologist and the archaeologist, however, is particularly liable to fall a prey to premature generalizations. Nevertheless certain conclusions from "spade history," as contrasted with written or legendary history, may be stated with considerable confidence.

- (1) There are many converging lines of evidence which point unmistakably to the great antiquity of man when measured by any historical time scale.
- (2) Man appeared in Europe at a remote time when climatic conditions were different from those at present, and when he was the contemporary of many kinds of animals now extinct.
- (3) In America the evidences of human antiquity, as yet discovered, by no means go back as far as in Europe and Asia, although the recently discovered flint culture of New Mexico, typified by unique fluted so-called "Folsom points," two of which were discovered embedded in the backbone of an ancestral bison in Texas, indicate the presence of man in America as far back as 15,000 to 25,000 years ago when bisons roamed the western plains.
- (4) The direct descent of *Homo sapiens* is not through any species of living primates, but is to be traced back to arboreal ancestors of very remote common ancestry.
- (5) Man is a part of the general evolutionary scheme that includes all life. As Dr. W. W. Keen once said in pointing out the reasonableness of this conclusion, "The laws of mathematics do not hold up to 1,000,000 and then give way to something else."

The Units of Structure—Cytology

I. THE CELL THEORY

It is quite essential in constructing any house of knowledge to know the units out of which the intellectual edifice is built. Thus, the chemist must know the elements from which his compounds are made, the writer must be acquainted with the alphabet, the mathematician with numerals, while the biologist must know the units that combine to form the diversities of living bodies.

The structural units with which the biologist deals are termed *cells*, and the science of cells is called *Cytology*.

Robert Hooke first suggested the word "cell" in 1665, when he described "little boxes or cells distinguished from one another" that he saw in thin slices of cork. The word is not a fortunate choice, however, suggesting as it does prison walls, for although "walls do not a prison make" neither do they adequately describe the biological unit. Nevertheless the term has come to stay and its use is now extended to indicate units of biological structure, regardless of whether the *walls* of a cell are in evidence or not.

The conception that all living creatures are made up of organic units, or cells, dates from 1838–1839, when Schleiden and Schwann, botanist and zoölogist respectively, published important investigations on the subject. The essential conclusions of the "cell theory" propounded by them, as now modified, are:

- (1) Every living thing is composed of organic units (cells), or products of their activity;
- (2) Every living thing begins life as a single cell;
- (3) Every cell is derived by a process of division from some preceding cell.

II. A TYPICAL CELL

A generalized diagram of a cell is represented in Figure 91. Within the cell is the *nucleus*, surrounded by a *nuclear membrane*. Outside of the nu-

cleus is the *cytosome*, or body of the cell, enclosed in a *cell membrane*. Within the cytosome may be embedded pigment granules, chondriosomes, crystals, oil-droplets, vacuoles, plastids, or other substances. Frequently there may also be identified in the cytosome a tiny body called the *centrosome*, from which delicate lines radiate in every direction.

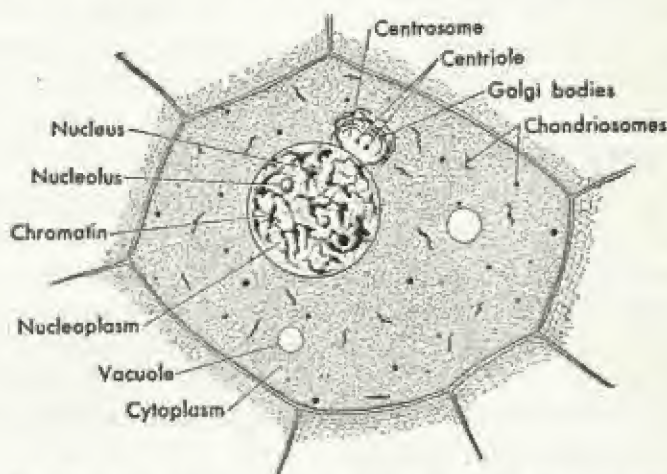


Fig. 91. Diagram of a generalized tissue cell. (From Huettnier, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

The nucleus is the headquarters of the whole organized unit, since changes which the cell undergoes are initiated there. It is made up of more than one substance, a fact that is revealed by applying certain stains which, through chemical union, affect parts but not the whole of the nuclear substance equally. That part most readily stained by certain dyes is called *chromatin*, or "colored material," and during certain phases of cell life the chromatin material masses together into visibly definite structures called *chromosomes*.

When cells crowd together during the formation of tissues, they become subjected to mutual pressure, so that their typical spherical shape becomes modified. Any of the several parts of a cell may undergo extreme modification, but most of the fundamental features outlined above, which make a cell an organized unit of living substance, characterize every cell.

III. CYTOMORPHOSIS

Cells are subject to the inevitable laws of change common to living things generally. The succession of changes through which each individual cell passes during its lifetime is termed *cytomorphosis*.

The term may be extended to include also the transformations through which successive generations of cells pass in the process of differentiation. Thus, in Lewis and Stöhr's *Histology* the following definition is given: "Cytomorphosis is a comparative term for the structural modification which cells, or successive generations of cells, undergo from their origin to their final dissolution. In the course of their transformation, cells divide repeatedly, but the new cells begin development where the parent cells left off."

The initial phase of cytomorphosis is characterized by a lack of specialization. This is followed by a series of progressive changes in which the cell becomes finally fitted for its life work, whatever it may be. After a varying period of usefulness, signs of old age appear; eventually the cell goes the way of all flesh and its dead remains are removed from the society of its fellows.

Some kinds of cells, like red blood corpuscles or epidermal cells, live a strenuous life, completing their entire cytomorphosis in a comparatively brief time, while others, like germ cells, may remain dormant for years in an undifferentiated embryonic condition before they finally move forward to fulfil their destiny.

There is much similarity between the life of a cell and of an individual. Both begin with a primitive generalized stage; both pass through expanding infancy and differentiating youth; both arrive at specialized maturity and usefulness; both wear out and die. In one particular, however, there is a striking difference. An *individual* reproduces its successors only when mature, that is, after it has become differentiated or specialized. A *cell*, on the other hand, reproduces its kind only while it is still in the comparatively undifferentiated embryonic phase of its life cycle, losing almost entirely the power to do this after it has attained specialization. The result is that many cell units of the body, for example nerve cells, having once gone through to the extreme end phases of their differentiation, lose the power to replace themselves with daughter cells. They have passed beyond the embryonic stage of cytomorphosis when replacement is possible, and after wearing out are unable to leave successors.

IV. CELL DIFFERENTIATION

The path of specialization that a cell follows in cytomorphosis is dependent upon the work it has to perform in the cell community of which it is a part.

A typical embryonic cell, uncrowded by neighbors, tends to be spherical in form but rarely has opportunity to remain so. Red blood cells of the lower vertebrates perhaps come nearest to retaining the original form of embry-

onic cells, because the work they do of rolling about through the blood channels of the body is facilitated by their round shape. Leucocytes, or white blood cells, frequently become irregular or amoeboid in form and have the ability upon occasion to change their shape. They are thus able to escape from the blood vessels by squeezing through between the cells of the capillary walls into surrounding tissues, where they nose their way between other cells to remove dead ones or to devour invading bacteria in their mission of sanitation.



Fig. 92. Various types of cells. A, smooth muscle cells; B, striated muscle fiber; C, cartilage cells; D, amphibian red blood cell; E, amoeboid white blood cell; F, nerve cell; G, ciliated epithelial cell; H, spermatozoan; I, squamous epithelial cells, surface view; J, fat cells; K, bone cell.

Squamous epithelial cells, whose business it is to cover surfaces, become flattened like shingles, while muscle cells, specialists in contraction, assume a much elongated form by which their function of shortening is best accomplished.

Detached cells like spermatozoa, that need to acquire the ability to travel in a fluid without having the propelling power of the heart back of them, as do blood cells, differentiate from the embryonic spherical form into a tadpole-like shape, becoming equipped with a powerful locomotor tail that drives them forward to their destiny.

Skeletal cells, the service of which is to furnish support or protection, develop an interstitial substance; while some secreting cells exhaust themselves at the expense of the cytoplasm in the production of their secretions. Extreme modification in form is seen in nerve cells where specialization has gone so far that it is hopeless to expect such cells ever to perform any other function than that to which they have become committed.

These examples of differentiation are only a few of the many guises in which the building blocks of organic structure appear.

Some type forms are diagrammatically indicated in Figure 92.

V. CHROMOSOMES

With the development of the compound microscope, the invention and utilization of aniline dyes and improved cytological technic generally, the presence of chromosomes within the cell nuclei became known, and the far-reaching importance of their peculiar structure unquestionably established.

It has been found (1) that chromosomes are probably always constant in number and shape in every cell of every individual of any particular species; (2) that they behave in a predictable way throughout all the vicissitudes of cytomorphosis; (3) that every cell not only comes from a preceding cell but every chromosome in the nucleus comes from a preceding chromosome like itself; (4) that during the changes of cytomorphosis when chromosomes apparently break up into indefinite masses, losing their characteristic appearance, they later reappear in the identical size, shape, and sequence of units that they formerly had; (5) that this behavior is evidence that their individuality is maintained and that they are not simply chance masses of unorganized stuff; and (6) that the various chromosomes of any cell not only assume characteristic shapes and sizes, but that they also occur in *pairs, two of each kind in every cell* excepting the sex chromosomes of many species.

VI. MITOSIS

The usual behavior of a cell during the period of increase when two cells form out of one, is called *mitosis*. The astonishing and intricate details of mitosis are generally unsuspected and quite strange to the uninitiated, although the process is occurring continuously in all living creatures, with countless repetitions. Upon its orderly performance depends every step that serves to differentiate any animal or plant, starting from the fertilized egg and including all growth and organic repairs. The founders of the cell

theory surely could not have imagined the extent of the vistas which their preliminary generalizations were destined to open up, for mitosis is a far more detailed and complicated performance than simply pinching the original cell in two.

The essential thing in cell division seems to be the equipment of each new cell unit with a complete set of chromosomes in its nucleus, duplicating in number, form, and size those of the parent cell. In the process of cell formation, which consists of a parent cell dividing into two daughter cells, the chromosomes play the leading part. A very brief and general description of the phases of a typical mitosis, with a series of explanatory diagrams follows, but it should be kept in mind that the stages described as distinct really merge into each other continuously, like a moving picture, and that the actual process of mitosis from start to finish will have repeatedly taken place somewhere within the bodily frame of the reader many times over during the studious reading of this paragraph.

Four general phases of mitosis are recognized as sufficiently distinct to mark well-defined changes from the "resting cell." These are known as the *prophase*, *metaphase*, *anaphase*, and *telophase*.

The *resting cell* (Fig. 93A) is characterized by the presence of a nuclear membrane and a chromatin network within the nucleus, as well as oftentimes also by a pair of centrosomes. In the beginning of the *prophase* (Fig. 93B-D) delicate *spindle fibers* appear between the centrosomes, and the chromatin is in the form of a threadlike *spireme*. As the prophase progresses the centrosomes move apart and the chromatin thread gives rise to separate chromosomes each more or less completely split into two.

In the *metaphase* (Fig. 93E) the chromosomes lie at the equator of the cell, being connected by spindle fibers with the centrosomes, each of which now occupies a polar position.

In the *anaphase* (Fig. 93F) these split chromosomes, each containing a sample of every different kind of substance that was distributed along the length of the parent chromosome, begin to separate from each other and to move towards the poles.

During the *telophase* (Fig. 93G) the elongated cell body begins to pinch in two, while the migration of the chromosomes towards the poles is completed.

Finally the division of the cell body into two parts enclosed in separate cell membranes becomes complete. The spindle fibers have disappeared and a nuclear membrane has re-formed around the chromatin network, derived from the chromosomes. Two resting cells take the place of the single one with which the quadrille of mitosis began (Fig. 93H).

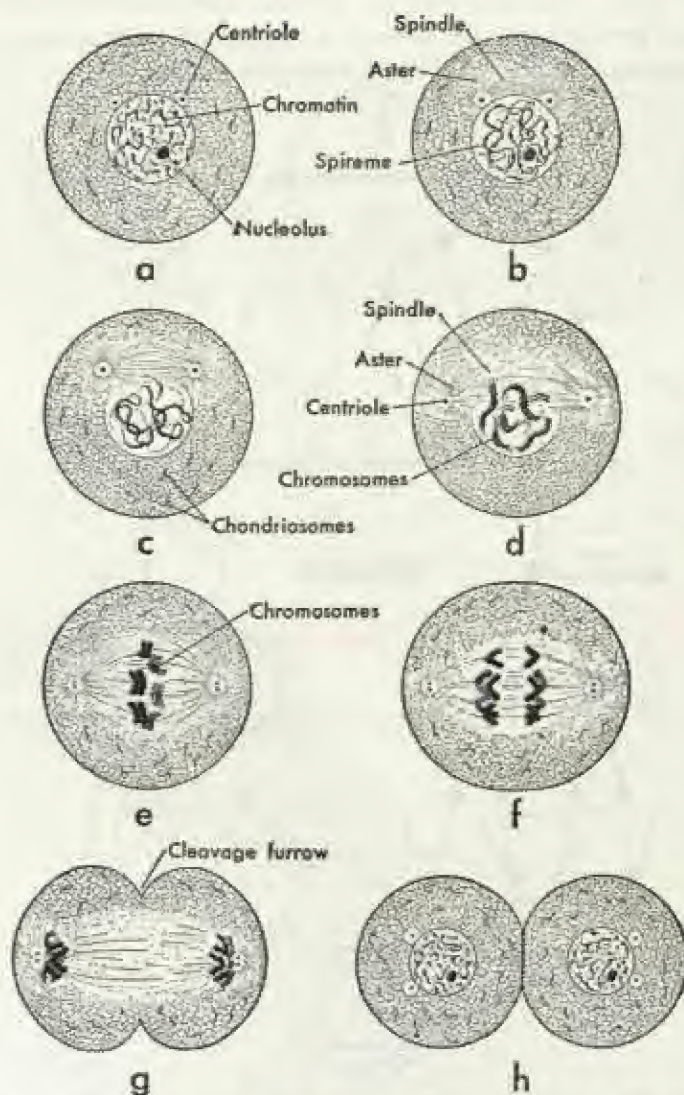


Fig. 93. Mitosis of an animal cell. *a*, interphase; *b-d* prophase; *e*, metaphase; *f*, anaphase; *g*, telophase; *h*, interphase. (From Huettnner, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

VII. FERTILIZATION

Mitosis makes clear how cells are derived from preceding cells. It does not account, however, for the process of vertebrate reproduction involved in the formation of a new individual from two parents.

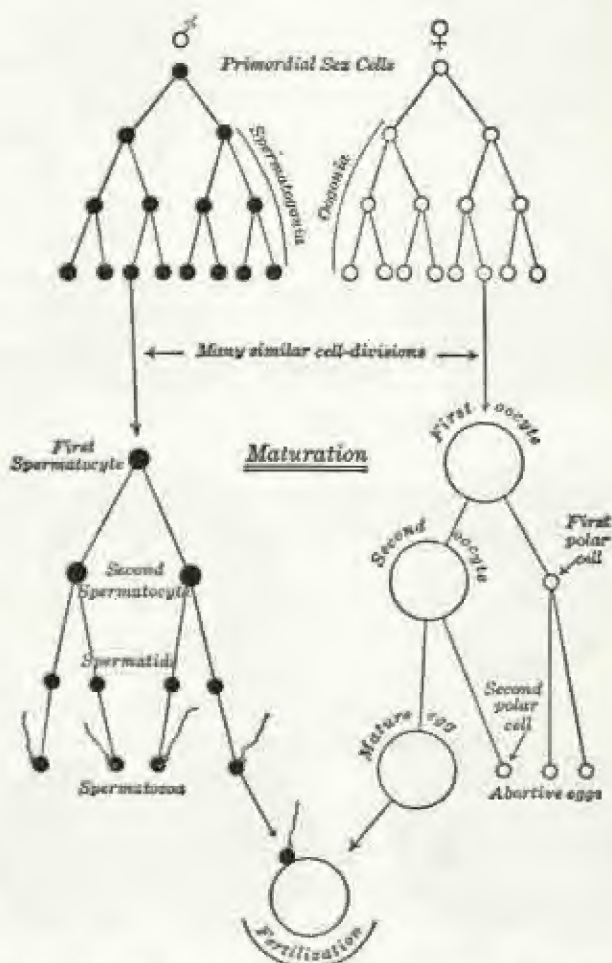


Fig. 94. Diagram to show typical maturation and fertilization.

Sexual reproduction, which is the prevailing means of numerical increase among higher animals and plants, involves something more than an unbroken succession of mitoses. The essential feature of it is the combination of the chromosomal resources of two cells, egg and sperm, to form an independent starting point for a new series of mitoses.

If mitosis can be defined as *making two cells out of one*, then sexual reproduction may be described as *making one cell*, that is, a fertilized egg, *out of two cells* (Fig. 94).

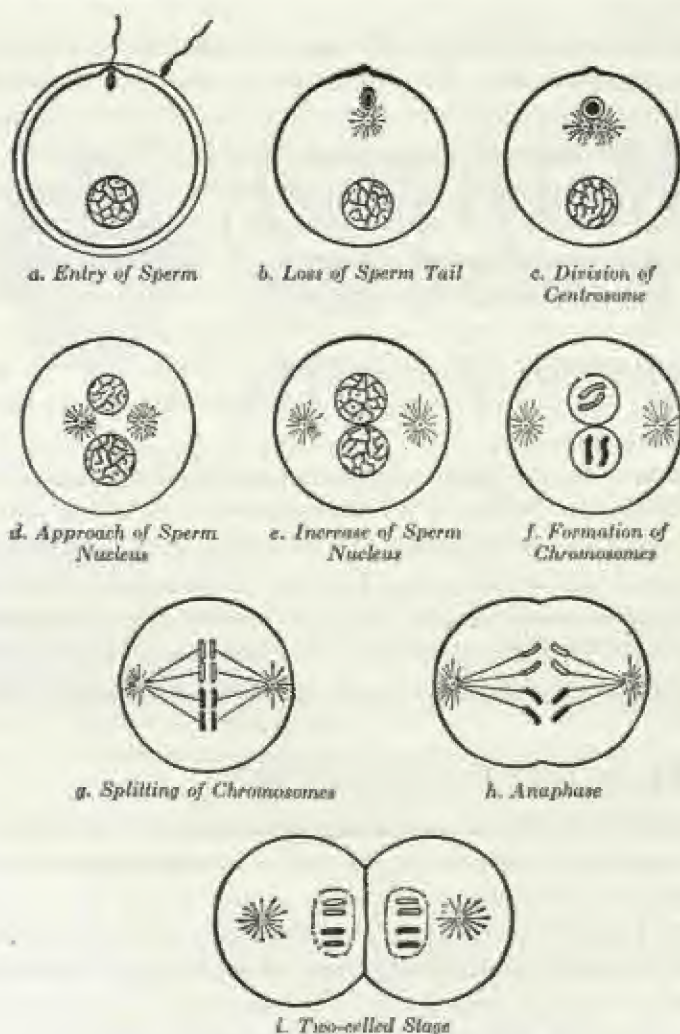


Fig. 95. Fertilization.

As has been shown, mitosis is an elaborate process by means of which the *same number* of chromosomes is maintained throughout all the successive generations of cells that make up an individual. When cells from two such individuals *unite*, some provision must be made for the reduction in the number of their chromosomes, else the cells of the new series of mitoses in the new individual will have double the typical number of chromosomes

for the species. This situation is met by a preparatory process of *maturation*, or "maturing," whereby the chromosomal material in each cell is cut in half. This process of the disposal of half of the germ-cell chromosomes is termed *meiosis*.

Meiosis includes two mitotic divisions, of a special type, following one another in rapid succession. Let us take as an example a species in which the general body cells contain four chromosomes. During ordinary mitoses of these cells the number of chromosomes is temporarily increased to eight; but, with the distribution of half to each daughter cell, the number immediately returns to four. In the same species the two meiotic divisions, which are always accompanied by only one period of chromosome-splitting, also have only eight chromosomes to distribute. The two successive cell divisions during meiosis, however, result in the formation of four cells and, with the equality of distribution typical of ordinary mitoses, each of these four granddaughter cells receives its share of the eight chromosomes, that is, two, the reduced number.

The union of the two germ cells, each equipped with the reduced number of chromosomes, results in the formation of a fertilized egg with the full complement of chromosomes, half of which were contributed by the mature egg and half by the sperm (Fig. 95). In basic plan, therefore, there is for each chromosome derived from the mature egg a comparable one from the sperm. Thus the chromosomes may be said to exist in pairs, each pair consisting of one member contributed by the male parent and one by the female.

VIII. THE DETERMINATION OF SEX

In man there are 23 pairs of mated chromosomes (*autosomes*) in each cell of the body and in addition in the male a mismatched pair of *sex chromosomes* (*allosomes*), sometimes known as x and y , making a total of 48 all together (Fig. 96). In the female besides the 23 pairs of autosomes there is a pair of allosomes, both of which are of the x type, likewise making a total of 48.

As a result of this inequality, when the sex cells undergo meiosis and reduce to one-half their equipment of chromosomes, the mature eggs are all alike ($23 + x$), while the mature sperm cells are of two sorts ($23 + x$) and ($23 + y$). The sex of the future individual is consequently dependent upon which kind of sperm unites with the egg, as follows:

egg	sperm	fertilized egg
$(23 + x)$	$+$ $(23 + x)$	$= (46 + 2x)$ ♀ (female)
$(23 + x)$	$+$ $(23 + y)$	$= (46 + x + y)$ ♂ (male)

There is one outstanding exception to the rule that all individuals of any particular species have the same number of chromosomes in every one of their structural units. Among many species there is found to be one more chromosome in each cell of the female than of the male, although curiously in birds as well as in butterflies and moths (*Lepidoptera*) the reverse is

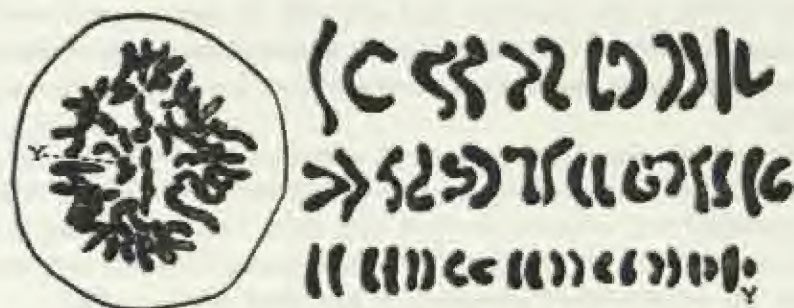


Fig. 96. Chromosomes of human male. At the left is shown the typical arrangement of 48 chromosomes on the equatorial plate of a spermatogonium. The smaller chromosomes are near the center. At the right the chromosomes from a somatic cell are sorted out and arranged in pairs. (After Evans and Swezy.)

true, the male showing one more chromosome than the female in each component cell. This sexual difference in chromosomal count occurs because the allosomes, instead of being represented in one sex by a mismatched pair, are present in that sex as an odd chromosome. In this case they are labelled x and o , the o indicating absence of an allosome. Determination of the sex of the resulting individual, however, comes out exactly as in the case of the mismatched allosomes, that is:

<i>egg</i>	<i>sperm</i>	<i>fertilized egg</i>
$(\text{autosomes} + x)$	$(\text{autosomes} + x)$	$(\text{double autosomes} + 2x) = \text{♀}$
$(\text{autosomes} + x)$	$(\text{autosomes} + o)$	$(\text{double autosomes} + 1x) = \text{♂}$

Still other combinations of allosomes have been observed, but although the number of allosomes and autosomes varies in different species of animals and plants, all cases agree in producing either *one kind of mature eggs*, and *two kinds of mature sperm*, or the reverse, so that the determination of sex in a new individual is referable to a definite combination of the chromosomes, making the chances fifty to fifty that either sex results, which agrees approximately with observed findings.

IX. A WORLD OF BILLIONS

The total number of cellular units taking part in the structure of the human body is beyond all imagination. Dr. Keen notes that the hair of a man's beard grows one millimeter in twenty-four hours. The constituent cells in the make-up of a millimeter of hair are, by count and computation, roughly 10,000, so that seven or eight new cells per minute are formed for every hair. Multiplying this number by the total estimated hairs of the head, one arrives at figures that even a mathematician has difficulty in comprehending.

The example given concerns but one of the many kinds of organic units which take part in the formation and repair of the human frame. When it is remembered that each one of these cells arises from a preceding cell by the elaborate machinery of mitosis, the laziest person may feel well assured that he has accomplished something at the close of every day.

Division of Labor in Tissues—Histology

I. TISSUES

Histology, or the science that deals with tissues, includes Cytology which was considered in the preceding chapter. The cells formed by successive mitoses from the fertilized egg differentiate into various tissues that constitute the body. A tissue is an association of similar cells which have undergone specialization for some particular purpose, and intercellular material, the amount of which varies greatly in different tissues. Thus, bone tissue includes bone cells, that are very much alike, and a considerable amount of hard intercellular material, while epithelial tissue is an association of epithelial cells, that resemble each other, but contain a minimum amount of intercellular substance.

The similar cells constituting a tissue may be connected with each other either by delicate strands of cytoplasm that penetrate the enclosing cell walls, or by an intercellular ground substance of some sort either secreted by the cells themselves in the form of exaggerated cell walls, or formed out of intruded interstitial material arising extraneously, like mortar between bricks.

Combinations of tissues make *organs* in much the same way that different textiles are combined into garments, and in turn organs make *systems*, just as different garments together make costumes. For example, the stomach is an organ that is assembled out of muscle tissue, blood tissue, gland tissue, nerve tissue, and the like, which together with other organs like the teeth, intestine, and pancreas, forms the *digestive system*.

For purposes of general description tissues may be classified as follows:

- I. Fluid tissues
- II. Stationary tissues
 - 1. Epithelial
 - 2. Connective
 - 3. Muscle
 - 4. Nerve

II. FLUID TISSUES

The fluid tissues are blood and lymph. Their cellular components are disconnected and are, therefore, constantly rearranging themselves with reference to each other, unlike the cells of other tissues which maintain a comparatively stable spatial relationship with each other.

In the lower invertebrates, such as the coelenterates and flatworms, the body fluid has no cells. Many invertebrates have only amoeboid white blood cells, but the blood of vertebrates generally is characterized by the presence of both white and red blood cells, and is consequently an elaborated fluid tissue.

Fluid tissues permeate the spaces which separate other tissues, and even the interstices between the cells of these tissues. They also occupy larger spaces, like the cavities of the joints, for example, and particularly circulate through special channels, called blood vessels and lymph spaces, that extend to almost every part of the body. In a later chapter, further consideration of the blood will be given.

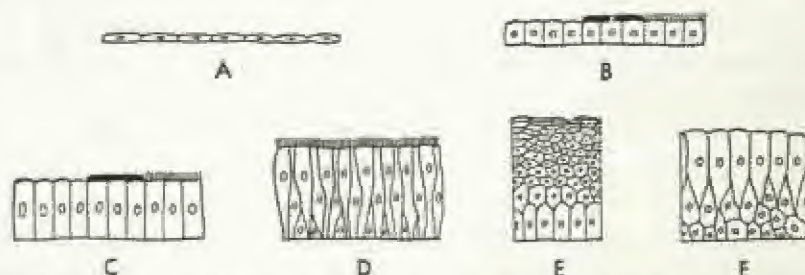


Fig. 97. Epithelial tissues. A, one-layered squamous (flat) epithelium; B, one-layered cuboidal epithelium, three cells with cuticle and three with cilia; C, columnar epithelium; D, pseudo-stratified ciliated columnar epithelium; E, stratified squamous epithelium; F, stratified columnar epithelium.

III. EPITHELIAL TISSUES

Epithelial tissues (Fig. 97) are the most primitive of all tissues. They come into contact with other stationary tissues *on one surface only*, since they clothe the outer surfaces of the body and line various cavities and passage-ways, including the blood vessels. They produce both cells that receive stimuli from the outside world and those that secrete and excrete different substances, as well as giving rise to the highly important sex cells.

There is usually a minimum amount of intercellular material in epithelial tissues. The cells composing them may assume a *squamous*, *cubical*,

or *columnar* form, and may be arranged in a single layer (*simple epithelium*) or a succession of layers (*stratified epithelium*).

Glandular epithelial tissues have a great variety of functions in the economy of the organism, namely, *digestive* in the salivary, gastric, and pancreatic glands; *defensive* in poison glands of snakes, and stink glands of skunks and other carnivores; *protective* in the mucous glands of fishes and amphibians, the shell-producing glands of mollusks, and the ink glands of squids; *lubricative* in the oil glands of the hair, and in mucous glands generally; *nutritive* in the mammary glands and in the albuminous glands of birds; *constructive* in the spinning glands of spiders and cocoon-forming insects; *cleansing* in the lacrimal glands of the eyeball; and *temperature-regulating* in the sweat glands of the mammalian skin.

When substances produced by gland cells are utilized for the benefit of the organism as a whole, they are defined as *secreting* glands, but if the substances produced are waste products that are cast out of the body, they are termed *excreting* glands.

If a gland is supplied with a duct whereby its products may reach the outside or be poured into some internal cavity or passage-way, it is termed an *exocrine* gland, but if no duct is present and the products of glandular activity must be transferred to the blood in order to be distributed, then it is known as an *endocrine* gland, and the substance which it produces, as a *hormone*.

The morphology and behavior of these various glands will receive more attention later. It is sufficient here merely to assign them to their proper place among the epithelial tissues.

IV. CONNECTIVE AND SUPPORTING TISSUES

Connective and supporting tissues of vertebrates lie usually inside of the integument that clothes the body. The component cells of these tissues do not form layers, as epithelial tissues tend to do, but are massed together with more irregularity. Their intercellular substances are usually much more in evidence, particularly in cartilage and bone.

1. Connective Tissues

Included among connective tissues, whose mission is filling space between organs and parts of organs, are at least five different sorts that may in some instances merge into each other, namely, (1) gelatinous; (2) notochordal; (3) reticular; (4) adipose; and (5) fibrillar.

Gelatinous tissue reaches its most characteristic expression in sponges,

and semi-transparent pelagic animals, such as medusae and ctenophores, in which the jelly-like bulk of the body is composed of secreted inter-cellular material throughout which are scattered a few cells, frequently joined together in a very open meshwork by delicate cytoplasmic bridges. This type of tissue does not commonly appear in the bodies of adult vertebrates, although during embryonic development the so-called mesenchyme passes through a gelatinous tissue phase.

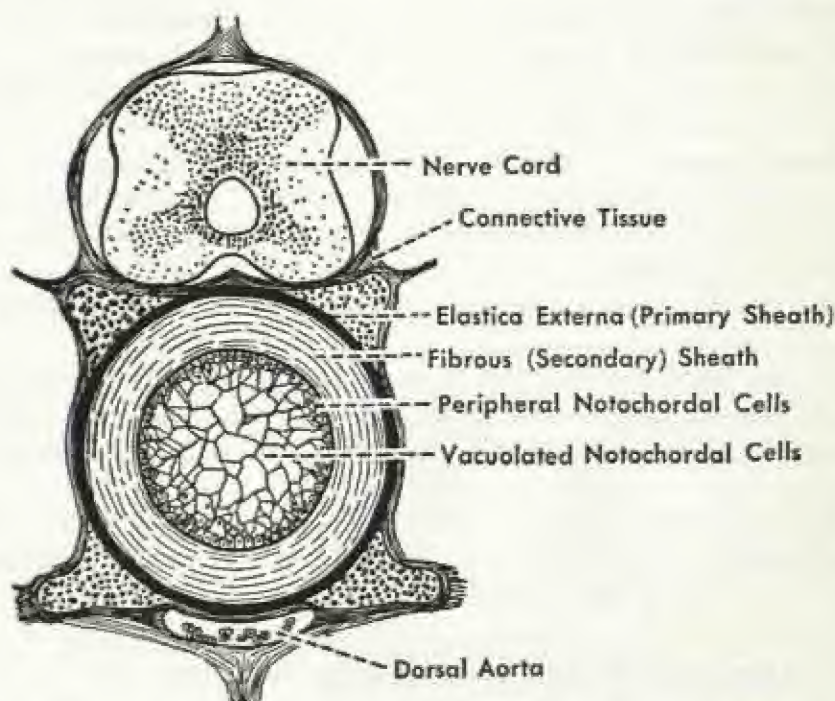


Fig. 98. Cross section through the notochord and its sheaths, from a young dogfish.

In *notochordal tissue*, on the contrary, there is a great reduction of intercellular material, so that the thin-walled cells lie closely pressed together (Figs. 98 and 211). Whatever rigidity is attained by this tissue is due largely to the fact that the cells are so tightly packed within a tough sheath that a certain turgor results like that when sausage meat is crowded into a casing.

Reticular connective tissues (Fig. 99) form the meshlike supports that characterize many of the softer organs, like the liver, spleen, and lymph nodes, which are ordinarily thought of as being without internal skeletal devices of any kind.

Adipose tissue is somewhat similar to the ordinary reticular tissue that forms the skeletal matrix of soft parts, for in this tissue groups of cells that specialize in fat storage lie enmeshed in a loose reticulum. When the fat cells are melted out of a piece of fat pork by frying, for example, there is left behind a residual network which is the skeletal, or reticular, part of the adipose tissue.



Fig. 99. Reticular connective tissue from a lymph gland of a cat, to show the supportive skeleton of a soft organ. (After Krause-Schmahl.)

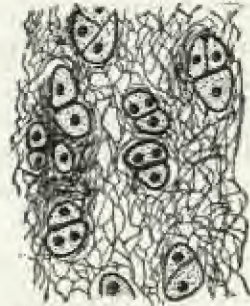


Fig. 100. Fibrillar tissue in the form of elastic cartilage from the external ear of man. (After Böhm, Davidoff and Huber.)

Like other connective tissues, *fibrillar tissue* (Fig. 100) consists of cells but it is distinguished principally by fibers that interlace among the cells. These fibers, themselves the product of cellular activity, are of two sorts, white non-elastic fibers, and yellow elastic fibers. The yellow fibers are peculiar to vertebrates. They occur in such parts of the body as the walls of the blood vessels, valves of the heart, the lining of the alveolae of the lungs, and in intervertebral ligaments. Both yellow and white fibers may be densely compacted together, as in *fascia* and *sheaths* of muscles, in *perichondrium* and *periosteum*, around cartilage and bone respectively, or they may be arranged in the form of looser texture, such as is found in the walls of blood vessels and the dermal part of the mammalian skin where they form the substance that is manufactured into leather.

In the *sclera* of the eyeball and in *tendons*, between muscles and bones, the fibers are mostly white. Fibrillar tissue plays an indispensable part in holding things together and is probably the most widespread tissue in the vertebrate body.

2. Supporting Tissues

(a) **Cartilage.**—Cartilage, or “gristle,” is a nerveless, bloodless, relatively flexible tissue that enters into the skeleton of vertebrates. Its texture

is not as firm and unyielding as bone, and consequently it is better adapted as scaffolding for water animals, such as fishes, where the surrounding medium helps to support the body, than for such use in land animals whose weight is held up in thin air.

There may be distinguished at least five kinds of cartilage, namely, (1) precartilagel; (2) hyaline; (3) fibrous; (4) elastic; and (5) calcified cartilage.

Precartilage is a temporary embryonic type that precedes the formation of other kinds, but may sometimes endure in the adult organism, as in the fin rays of certain fishes. It consists of cells (*chondroblasts*) that have the power to secrete a thickened cell wall, or an intercellular matrix, at the expense of their own cytoplasm.

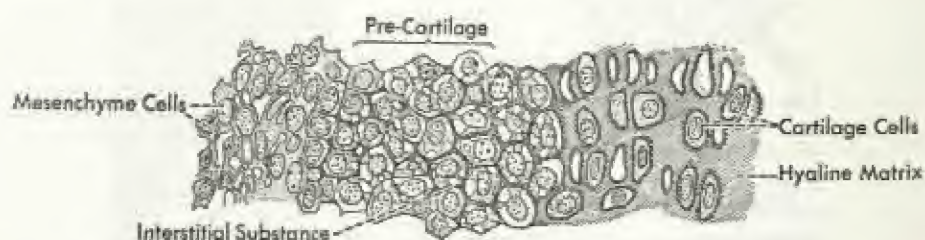


Fig. 101. The differentiation of hyaline cartilage, earliest stage at the left. (After Maximow and Bloom.)

When this process has continued until the diminishing cells have isolated themselves from their neighbors in a sea of surrounding matrix, which is somewhat firm and translucent, the *hyaline* stage has been reached (Fig. 101). Hyaline cartilage is found in the bendable and projecting part of the human nose, at the ends of the ribs joining the breastbone, in the stiff incomplete rings that keep the tracheal and bronchial tubes from collapsing, and in other parts of the bodily structure.

The matrix between the cartilage cells may be interwoven with fibers, either white or yellow, as in fibrillar connective tissue, in which case either fibrous or elastic cartilage is the result. *Fibrous cartilage* is typically represented by the padlike intervertebral discs separating the centra of the vertebrae in the backbone, while *elastic cartilage* is found in such places as the epiglottis, and the pinna of the external ear which fortunately springs readily back into its original shape when distorted.

Sometimes the intercellular matrix of hyaline cartilage becomes infiltrated with limy salts, when it is designated as *calcified cartilage*. In adult cartilaginous fishes much of the cartilage is of the calcified type.

(b) **Bone.**—Bone is the best known of the skeletal tissues of vertebrates. As contrasted with cartilage it is supplied with nerves and blood vessels, and is considerably more rigid. It includes at least two kinds of cells, *osteoblasts* and *osteoclasts*. The first of these are *bone-forming cells* which produce the limy intercellular matrix that characterizes bone. The osteoclasts, on the other hand, are *bone-wrecking cells*, that tear down bone tissue and make possible the rearrangement of material necessary to the accomplishment of growth among such unyielding building materials as bony plates.

Bone consists of two essential substances: (1), an organic base of living cells, and (2), in the excessively developed matrix surrounding these cells, an infiltrated mass of inorganic limy salts. These two components are so intimately joined that there is no visual way of separating them, yet each alone is sufficient to give characteristic contour to a bone, for when the organic part is burnt out by fire, or the inorganic component is dissolved away by acid, the part remaining in each instance preserves the original form of the bone.

In relative weight the inorganic, or mineral, part of bone is about three fourths of the whole, although the ratio of inorganic to organic varies with age, ordinarily becoming greater the longer the bone lives. According to Heintz an analysis of the mineral constituents of a human femur resulted as follows:

	<i>Per Cent</i>
Calcium carbonate	9.06
Calcium phosphate	85.62
Magnesium phosphate	1.75
Calcium fluoride	3.57
	<hr/> 100.00

The embryonically active *osteoblasts* are responsible for the formation of bone tissue. By their rapid multiplication living bone cells are formed which in turn secrete the hard parts, or *lamellae*. As bone grows, however, it becomes necessary not only to add new tissue but also to remove that which has already been formed. Comparing the lower jaw of an infant with that of an adult (Fig. 102), it is evident that no single cell of the former structure can persist unchanged throughout the process of growth. The jaw of an infant is not simply added to as it becomes larger, but all the building material composing it must be broken down bit by bit and reassembled, and supplemented many times before the adult bone is fashioned. It is as if a

stone building were enlarged not simply by adding to the outside of it as it stands, but by tearing it down and reassembling it with additional stones in order to enclose a larger area.



Fig. 102. Diagram comparing the jaw of an infant with that of an adult. (After Kölliker.)

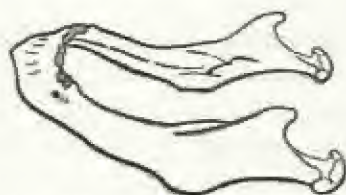


Fig. 103. The condition of the jaw in old age, showing the acute projection of the chin resulting from the loss of teeth and the absorption of the sockets for the teeth.



Fig. 104. In toothless old age the chin and the nose tend to hobnob together. (After Camper.)

This wrecking of bone tissue already formed in order to make way for rearrangement and enlargement is accomplished by the rather large definitely identified cells called *osteoclasts*. The destructive work of these cells is not always followed by equally constructive reorganization, however, for when the work of the osteoclasts exceeds that of the osteoblasts, a bone decreases in size. Thus, in toothless old age (Fig. 103), the lower jaw not only becomes smaller through the loss of teeth, but the bony sockets in which the teeth were set also decrease in size through the removal of tissue by osteoclasts, with the result that the chin and nose tend to hobnob together (Fig. 104).

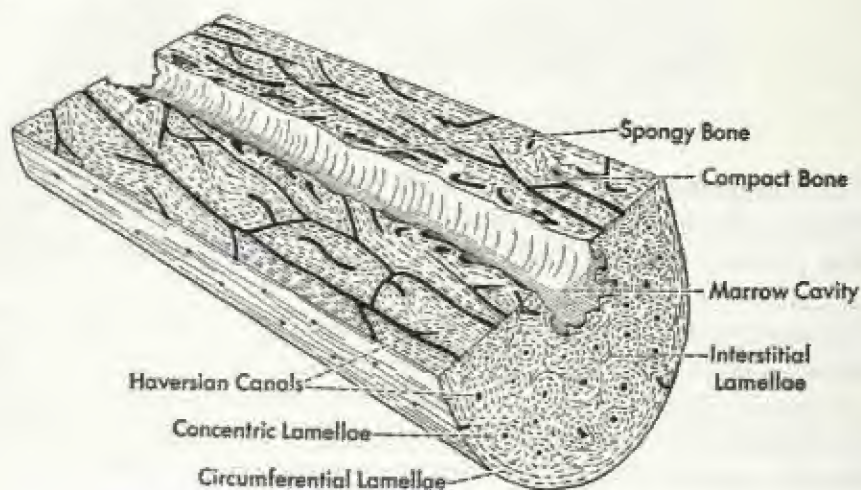


Fig. 105. Stereogram of bony tissue.

When a thin slice of bone is taken from a cross section through the shaft of the femur, for instance, and ground down to translucent thinness, if examined under the microscope, it is seen to be made up of innumerable small bony plates, or *lamellae* (Fig. 105). Even to the naked eye there are two kinds of bone, namely, spongy and compact. In *spongy bone* the lamellae are arranged in an open framework leaving many spaces filled with bone marrow. *Compact bone* appears solid but actually includes many minute spaces, in which cells lie or through which blood vessels and nerves run. The lamellae are arranged in at least three different ways, concentrically, interstitially, and circumferentially.

Concentric lamellae, somewhat like rings of growth around the pith of a woody stem, envelop small tubelike branching passage-ways, the *Haversian canals*, which permeate the bone lengthwise, forming the conduits for the passage throughout the bony tissue of capillaries, lymphatics, and nerves. The Haversian canals, surrounded by concentric lamellae, are best seen in the dense tissue of the cylindrical shafts of the long bones in the appendages, where they communicate both with the periosteal coverings of the bone on the outside and, through the entire bony tissue, with the marrow cavity inside. They constitute the subways for organic traffic throughout the bone tissue, making this part of the skeleton a living adjustable structure.

Interstitial lamellae are necessarily irregular since they fill in spaces between neighboring Haversian systems.

Finally, *circumferential lamellae* are arranged either around the outside margin of the whole cross section of the bone shaft, just beneath the periosteum, or as an internal layer grading over into the spongy tissue that borders the marrow cavity within the bone.

The Haversian canals are not the only spaces between the lamellae that help to make the living bone porous. Between the hard lamellae separating them from each other are tiny spaces, called *lacunae*, or "little lakes," in which lie imprisoned the living bone cells (Fig. 106). Lacunal spaces communicate with each other through *canaliculi*, microscopic passageways through the walls of the limy lamellae.



Fig. 106. A diagram showing a fragment of bone tissue at the edge of an Haversian canal, through which blood vessels and nerves penetrate the substance of the bone. Eight lacunae, each containing a bone cell, are indicated and also their connection by *canaliculi*. The bony lamellae are represented in black.

Most hard parts of the skeleton are laid down first as connective tissue, followed by cartilage which is later slowly replaced by bone. These are *replacing* or *cartilage* bones. A few parts, notably the flat bones of the skull, are laid down directly in connective tissue membranes without a cartilage intermediary. To these the name *investing* or *membrane* bones is applied. In either case the hard parts are produced by connective tissue cells which

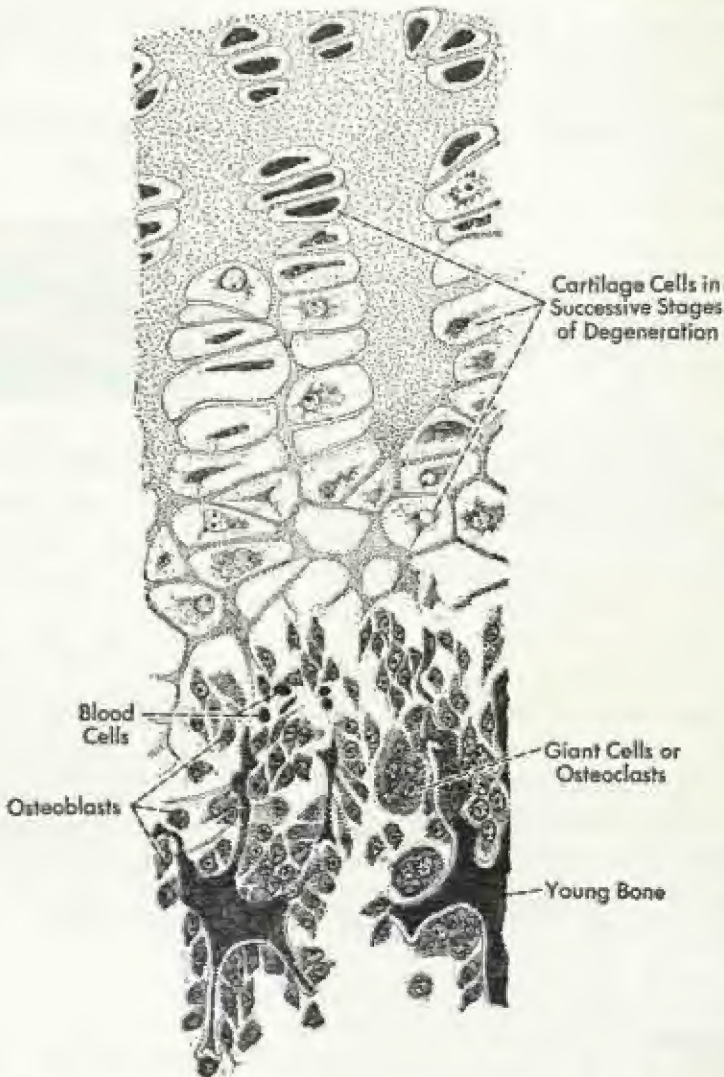


Fig. 107. Reconstruction of cartilage into bone. Beginning at the top of the figure, the cartilage cells are in successive stages of degeneration. (From Dahlgren and Kenner.)

acquire the ability to produce cartilage or bone. Although at first all of the bony tissue is of the spongy type, a thick region on each surface is later converted into compact bone, leaving inside a filler of spongy tissue in which the spaces are occupied by bone marrow. The connective tissue membrane which remains as a covering of the bones is called the *periosteum*.

In the case of a replacing bone like the tibia of the lower leg (shank), a cartilaginous rod is laid down in the connective tissue. Later this cartilage is replaced by bone in somewhat the following manner. Some of the perichondrial cells and others inside of the cartilage near the middle of the rod become bone builders (*osteoblasts*) and lay down a ring of bone at that point. Adjacent to this ring the cartilaginous matrix begins to dissolve, probably under the influence of certain cells which have been called *chondroclasts*. As fast as the cartilage is destroyed, spongy bone takes its place (Fig. 107). From the middle of the bar these changes spread toward the ends until the entire shaft (*diaphysis*) has ossified leaving only the ends (*epiphyses*) of the tibia as cartilage. This is the condition in man at about the time of birth. Soon after birth a center of ossification appears in each epiphysis

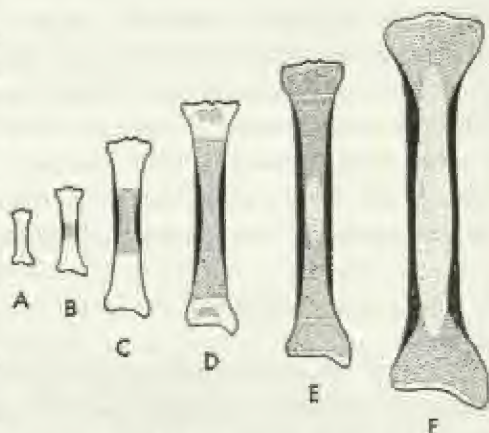


Fig. 108. Ossification and growth in a long bone of mammals. A, cartilaginous stage; B and C, laying down of endochondral bone (dotted) and perichondral bone (black); D, appearance of an ossification center for an epiphysis at each end; E, beginning of formation of marrow cavity (lighter dotted); F, fusion of epiphyses with shaft, leaving cartilage only at articular ends. (After Arey.)

and enlarges until the only cartilage left here is a cap on the articular surface and a plate between diaphysis and epiphysis (Fig. 108). The articular caps remain throughout life but the plate is a temporary device to permit elongation of the bone. The cartilage in the middle of the plate continues to grow and expand. At the same time the process of minute replacement goes on at the two surfaces where it is in contact with diaphysis and epiphysis. At an age of 17–25 years the cartilage of the plate ceases regeneration and the invasion of bone completely replaces the plate. The bone has then completed its elongation. During this developmental period there is also an increase in the diameter of the bone, by the addition of material on the surface. At about the time of birth *osteoclasts* commence to

destroy the bony plates in the center of the shaft leaving only the soft marrow which, from the beginning, is in between the plates. A large *marrow cavity*, running the entire length of the shaft, thus develops. This cavity slowly enlarges as the bone increases in length and diameter. During this same period the rest of the spongy bone of the diaphysis, but not of the epiphysis, is reorganized into compact bone laid down in concentric rings around the numerous small blood vessels which run through the bony tissue, thus forming Haversian systems.

In this manner the adult condition of the bone is reached. In the long bones the diaphysis consists of compact bone surrounding a large elongate marrow cavity. The epiphyses remain as spongy bone except for a very thin, outer layer of compact bone, which may not completely cover these parts. The spaces in this spongy bone are continuous with the marrow cavity and, as previously mentioned, filled with marrow. The connective tissue covering, which was called perichondrium in the cartilage stage, becomes known as periosteum where bone is present beneath it.

V. MUSCLE TISSUE

One of the commonest manifestations of life is movement. Even in stationary plants living cytoplasm streams about within the cells, and fluids are passed from one part to another. Within the animal body certain members of the cell community, like blood cells, shift about with much freedom, while other kinds of cells, leucocytes for example, are liable to change their shapes. The well-nigh universal ability of living cells to move or change shape, culminates in *muscle cells*, whose conspicuous contractility not only causes internal movement but exercises an influence for motion also in more or less distant parts of the body to which they are directly or indirectly attached.

The cytoplasm of the elongated muscle cells is differentiated into *sarcoplasm* and *myofibrils*, as well as sheaths which clothe the sarcoplasm like a thin rubber glove. Myofibrils are embedded in the sarcoplasm and are the particular mechanism of contractility. They are peculiar in that they effect contraction in only one direction instead of in any direction, as in the case with ordinary contractile cytoplasm. Muscular movement is always brought about by the *pull* of muscles, while restorative movements are in turn effected by the pull of antagonistic muscles, and not by the relaxation that follows contraction. Muscle tissue is, therefore, simply specialized tissue in which the general function of contractility is carried out more effectually than elsewhere.

Dr. A. E. Shipley has vividly emphasized the power that may be stored in muscle tissue by citing the performance of a jumping flea. Some patient person who succeeded in weighing nine fleas found their average weight to be 0.38 milligrams. Fleas can leap from 8 to 13 inches. If a man who weighs 70 kilograms, or about 150 pounds, made a corresponding leap, he "could leap to the moon in about ten jumps."

There are three kinds of muscle tissue that differ in the degree or manner of differentiation, namely, smooth, striated, and cardiac.

1. Smooth Muscle

Smooth muscle cells have a single nucleus near the center of the cell, are usually spindle-shaped, and rarely forked at the ends (Fig. 92A). In man they vary in size from 15 micra (15/1000 of a millimeter) in blood vessels, to 200 micra in the digestive tube, while in the walls of the uterus during pregnancy they may reach 600 micra in length. In the pliant walls of the bladder they are more or less interlaced or felted together, lying in every direction, so that the bladder when it is emptied contracts like a toy balloon rather than collapsing like an empty hot-water bag.

Smooth muscle cells are often isolated or in thin layers, or more rarely massed together into bulky tissues. They are widely distributed throughout the body, and are found for example in the skin where they act as hair-raisers, feather-fluffers, or around the openings of glands where they act as doorkeepers. They also form a large part of the contractile walls of various tubes and passage-ways, such as blood and lymph vessels, the digestive tube (except the upper part of the esophagus), the trachea and bronchi, the reproductive ducts, and the ureters.

2. Striated Muscle

Striated muscle tissue is "flesh," and in man it constitutes approximately fifty per cent of the weight of the entire body (Fig. 92B). It is found not only in the bulky body wall, and the muscles of the limbs where it effects locomotion, but also, at least in the higher vertebrates, in the diaphragm, tongue, esophagus, pharynx, larynx, and the muscles of the eyeball.

The component fibers of striated muscle tissue, which are quite evident in cooked corned beef, are commonly large, elongated cells that are no longer able to be served, like smooth muscle cells, by a single nucleus. In consequence scattered along the fiber many nuclei are present, like substations.

The descriptive term "striated" refers to the fact that the embedded elastic *myofibrils*, which extend throughout the length of the fibers, are dif-

ifferentiated into alternate beadlike bands lying side by side across the bundles of fibers in such a fashion as to produce a striated effect. These beadlike parts of myofibrils are physically and chemically unlike the connecting parts between the "beads," because they stain differentially with aniline dyes and refract light differently, the dark beads, or *anisotropic bands*, being doubly refractive in polarized light, while the *isotropic bands*, or parts between the beads, are singly refractive in polarized light.

Moreover there is a physiological difference, as well as physical and chemical, in these parts of the contractile fibrils within a muscle fiber, since anisotropic bands shorten more than isotropic bands during contraction.

In birds the "white meat" of the breast is characterized by an excess of myofibrils, while the "dark meat" has more sarcoplasm and less myofibrillar substance in its fibers.

In general the striated muscles effect quick movements of comparatively short duration and are *voluntary*, that is, under the control of the will, while smooth muscle tissue is *involuntary* and much slower in action. There are certain notable exceptions to this generalization among invertebrates, for the body muscles of some mollusks are smooth and voluntary, while the visceral muscles of insects and crustaceans are typically striated and involuntary.

3. Cardiac Muscle

The tissue of the muscular vertebrate heart is intermediate in character between smooth and striated muscle, in that the component cells are comparatively short, branching, and involuntary in action, although striated in appearance and multinuclear (Fig. 109).

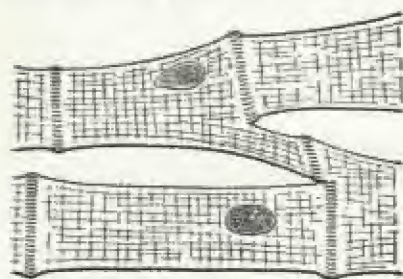


Fig. 109. Cardiac muscle cells.
(After Szymonowicz.)

The enormous dynamic force exercised by any kind of muscle tissue is seldom realized. The tireless heart of man, for example, knows no rest, as one ordinarily thinks of rest, but throbs faithfully day and night without skipping a beat throughout a long lifetime.

VI. NERVE TISSUE

Nerve tissue is characteristic of animals rather than plants, although the nervous function of sensitivity is a fundamental property of cytoplasm, by no means absent from plant life. This tissue consists of specialized nerve

cells, or *neurons*, accompanied by nutritive components of various sorts, connective tissue, and non-nervous supporting *neuroglia cells* of ectodermal origin. The cytoplasm of neurons is differentiated by the presence of *neurofibrils*, that differ from the rest of the cell in chemical composition, as shown by staining methods, and which are particularly fitted for reception of stimuli and the transmission of impulses, just as myofibrils are specialized instruments of contractility in muscle cells.

Neurons exhibit extreme modification from the characteristic spherical embryonic form, the cytoplasm being drawn out into extremely elongated processes or fibers of two kinds, called respectively *dendrites* and *neurites*. Dendrites are numerous and branch freely like a tree, as their name indicates, while there is only a single neurite to each cell (Fig. 92F).

When impulses travel through a neuron along the neurofibrils, they do not go at random in any direction but always enter through dendrites and pass out through the neurite. Impulses are relayed from cell to cell by chain-like contact (*synapse*) between the neurite of one neuron and the dendrite of the next.

"Nerves" are bundles of neurites and dendrites that extend like cables outside of the central nervous system. They are enclosed in a common sheath of connective tissue. *Ganglia*, also outside of the central nervous system, are aggregates of cell bodies of neurons.

Nervous tissue accomplishes a double mission: first, that of relating the organism to its environment through sense organs; and second, that of regulating and correlating the bodily activities by means of the central and autonomic nervous apparatus.

The Development of the Individual— Embryology

I. THE STARTING POINT

No animal or plant is an orphan in the sense that it has no parents. In protozoans produced by fission the parent perishes by division into progeny. The spontaneous origin, even of the most minute organisms, at least under present conditions on this globe, has been effectually disproved. Modern control of bacterial diseases, together with the incalculable boon of aseptic surgery and antiseptic practice, depends upon the clear understanding of this fact.

A new organism may be introduced into the brotherhood of living things by one parent or by two, but no animal or plant comes into the world of today unsponsored by preceding life.

When there is only one parent the new individual is said to arise by *asexual* reproduction. The method of *sexual* reproduction, however, that involves a double source, is by far the commoner way for higher animals and plants to begin their separate existence.

The starting point of a sexually produced individual is a *zygote*, or fertilized egg, which is a combination of two parental *gametes*, or mature sex cells. It is the purpose of this chapter to trace some of the more important episodes in the "miraculous pageant of transformations" that take place between the setting up of the *zygote* and the establishment of the adult organism. A fascinating part of biology is the particular province of *Embryology*, some familiarity with which is essential to the understanding of the structure and functions of adult animals and plants.

Ever since Aristotle described what he saw when he opened hen's eggs at various stages of incubation, embryology has been occupied with recording *what changes take place during development*, with the result that a considerable body of detailed information has been accumulated. In recent

years embryologists have not been content simply to find out *what* happens in a transforming embryo, and *how* the changes occur, but have sought more and more to explain *why* such changes take place. This attempt has led to *Experimental Embryology*, an aspect of biological science with alluring vistas that is claiming much attention today.

Why does the power to regenerate lost parts decrease as we go up the vertebrate scale? *Why* does the orderly sequence of development sometimes become upset so that a monstrous organism results? *Why* do groups of cells sometimes go on a rampage and form unorganized cancerous growth that the animal cannot control?

II. THE NECESSARY PARTNERS

1. Differentiation of the Germ Cells

Two germ cells, sperm and egg in animals, are necessary partners in the enterprise of a fertilized egg. The fact that different terms, namely, *pollen grains* and *ovules*, are commonly employed to designate the reproductive units in sexual plants does not indicate any essential difference in the germ cells of plants and animals. A pollen grain is a spore which produces an organism, the *pollen tube*, from which a fertilizing element or cell, homologous with the animal sperm, passes to the ovule.

Fertilization is the union of two diverse germ cells, and consequently provision has to be made for getting them together.

The egg, which is ordinarily loaded with first-aid nutriment for the future organism during the critical early stages of its development, tends to become relatively heavy and stationary, thus throwing upon the sperm the responsibility of doing the traveling in the necessary process of getting together. The egg does not meet the sperm half way. The sperm has to travel the entire distance. This circumstance has brought about a high degree of morphological difference in the germ cells of the two sexes.

2. Kinds of Sperm

The result of the physiological necessity of a union of germ cells to effect fertilization is that the sperm cells of animals, and the male cell in the pollen grains of plants, become specialized into structures adapted particularly for locomotion. In animals this involves a fluid medium in which to travel. In plants the traveling male germ cell within the pollen grain is more often adapted for transport through the air by the wind or through the agency of insects.

A typical sperm cell adapted for locomotion along a fluid highway is

pictured in Figure 92H. The human sperm cell, according to Waddington, can travel at the rate of about an inch in three minutes.

The differentiated *head* of the sperm, which is principally made up of the nucleus, carries the chromosomes that are freighted with the hereditary determiners, while the *middle piece* and the locomotor *tail* represent transformed cytoplasm, modified for particular uses. An animal sperm is thus adapted for sculling forward through a fluid medium by means of the vibratile tail. Animals never employ aerial routes for this purpose as do plants.

Among vertebrates, bony fishes and anurans usually broadcast their eggs and sperm in water, and the sperm cells travel in this medium to reach the egg. Among land forms like reptiles, birds, and mammals, internal fertilization occurs, so that the sperm travel up the oviduct to the egg in a secreted fluid medium that serves the same purpose as water in the case of aquatic animals. *Copulation*, which occurs in all land animals, is simply a device for insuring placement of locomotor sperm cells in a suitable highway leading to the waiting egg.

An exception to the almost universal type of sperm with a locomotor tail is found among certain worms, *Ascaris* for example, and in crabs, where an amoeboid or angular form is assumed by the sperm cell. The approach to the egg in this instance is accomplished by much slower movements, the creeping sperm being in contact with solid objects.

3. Kinds of Eggs

The eggs of animals differ specifically with reference to the load of nutritive yolk which they carry. Curiously those with a minimum amount of stored food are found at the two extremes of the chordate scale, namely, the eggs of amphioxus and of mammals. The eggs of amphioxus probably represent a primitive condition in the matter of the acquisition of yolk. The poverty of yolk in the small eggs of mammals has doubtless come about through a different chain of causes, correlated with the fact that not much stored food is required in the eggs of this group, since they early become implanted like parasites in the uterine wall of the mother from whom they derive their necessary nutritive start in life. As a consequence of the scarcity of yolk, the mammalian egg is remarkably small, that of man measuring only about $1/125$ of an inch in diameter (Fig. 110). As the yolk is scattered equally through these eggs, they are described as *isolecithal* (*iso*, equal; *lecithin*, yolk).

In cyclostomes, fishes, and amphibians, the abundant lifeless yolk is massed in the lower or "vegetal" half of the egg while the nucleus and

most of the living cytoplasm, constituting the embryogenic or "animal" pole, appears on the upper side. Such eggs are therefore *telolecithal* ("end-yolked").

So much yolk is present in the telolecithal eggs of reptiles and birds that the nucleus of the egg cell, together with its tiny halo of active cytoplasm, forms only a small area, or *germinal disc*, at the animal pole. When unhindered the heavy yolk invariably rotates so that the germinal disc comes to lie uppermost.

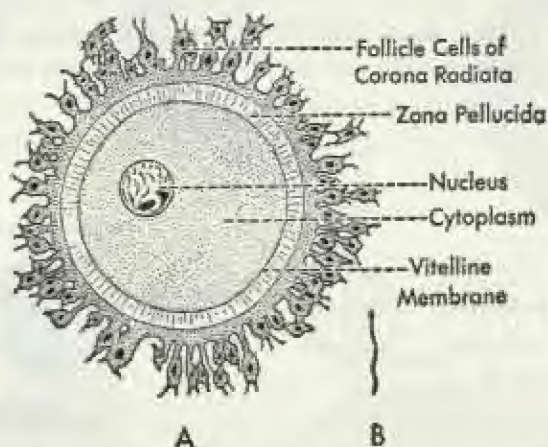


Fig. 110. A, human ovum, approaching maturity, much enlarged. B, human sperm, correspondingly enlarged. (After Arcy.)

In addition, birds have a reserve food supply of nutritive albumen or "white," packed around the egg within the protective shell.

If one stretches the point to include such accessory food material, the bird's egg must be regarded as the largest kind of all animal cells. The egg of the wingless *Apteryx* of the Antipodes weighs nearly one fourth as much as the entire bird. An ostrich's egg is equivalent in bulk to about a dozen hen's eggs, while that of the gigantic "moa," now extinct (Fig. 51), had twelve times the content of an ostrich's egg and might, therefore, easily hold the palm as being the largest animal "cell" ever known.

III. DEVELOPMENT OF A CHORDATE

The manner of development of an egg is dependent upon the amount of inert yolk that is present. In amphioxus, where there is very little yolk to hinder the process of orderly cell division, the entire egg mass is equally involved in cell formation, and early development is less complicated than

in most vertebrates. Before considering specific points for several representative chordates, let us first examine the fundamental plan of chordate development.

1. Cleavage (Segmentation of the egg)

After the union of the sperm and egg, the first of a long series of processes that transform the fertilized egg into an adult individual occurs. This first process, called *cleavage*, consists of a rapid succession of mitoses in which the initial cell becomes divided in turn into two, four, eight, and so on (Fig. 111), until a small mass of cells results, without appreciable increase in total weight over that of the fertilized egg. Each one of these small cells contains a complete double set of chromosomes, bearing hereditary potentialities from two parents, thus duplicating the original complement in the fertilized egg.

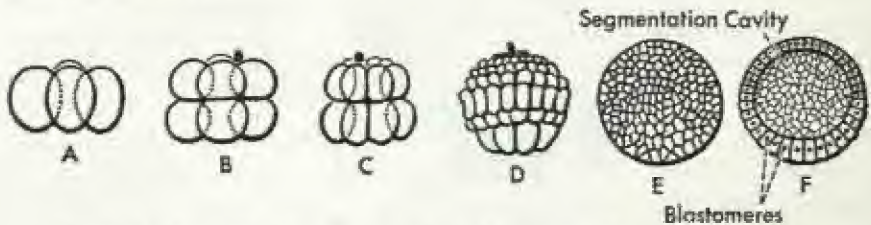


Fig. 111. Stages in the segmentation of the egg of amphioxus, terminating in the formation of the blastula (ϵ) which is shown in hemisection at ϵ . (After Hatschek.)

The result of these rapid preliminary cleavage divisions is the breaking up of the original cell into many separate working units. A very fundamental principle underlying differentiation is *division of labor*, and this is facilitated when there are different nuclear centers present for the initiation of different cellular enterprises.

2. The Blastula

As the small cells, of essentially uniform size, become more numerous, they arrange themselves in the form of a hollow sphere, or *blastula*, the cavity within being known as the *segmentation cavity* and the individual cells, *blastomeres*.

3. The Gastrula

The cells at one pole of the hollow sphere divide oftener and become more numerous and crowded than at the other pole. Since they remain in contact with each other without changing their relative positions to any

great extent, they tend to form a continuous layer that is more than sufficient to make up the original surface of the sphere in this region. They are, therefore, forced to find more standing room which is accomplished by their pushing into the segmentation cavity, with the result that a double cup, or *gastrula*, is formed (Fig. 112).

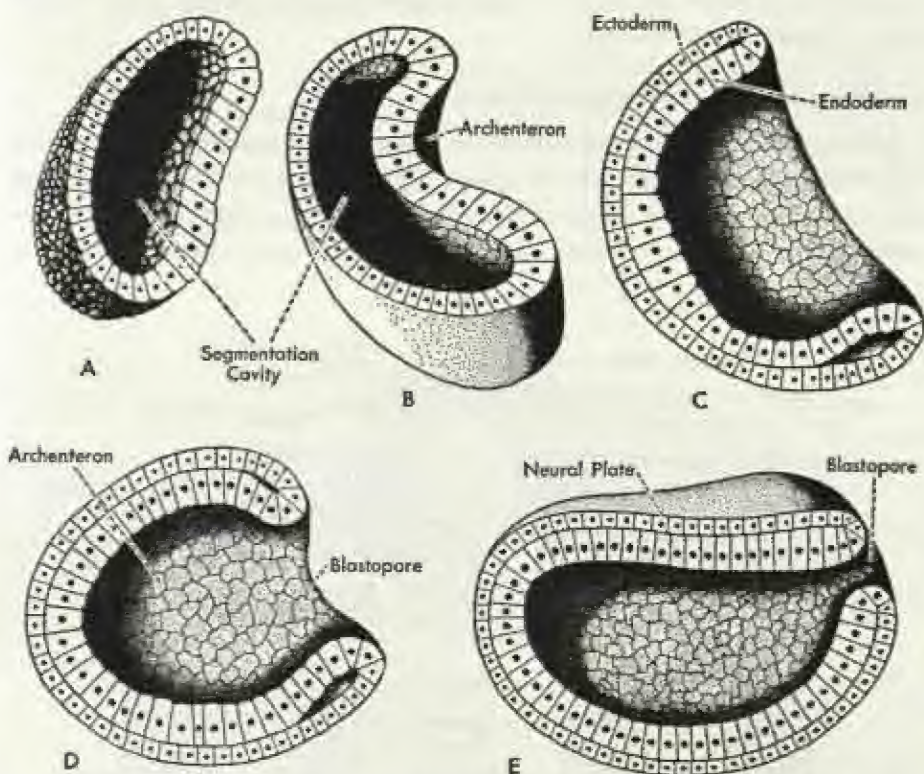


Fig. 112. Gastrulation in the development of *amphioxus*. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

The outer layer of this cup is the *ectoderm*, the inner layer the *endoderm* (or "entoderm" of some authors). The new cavity within the cup is termed the *archenteron*, or primitive digestive cavity, and its opening to the exterior, the *blastopore*. The latter is at the posterior end of the embryo.

The inpushing (*invagination*) of the endoderm continues until the segmentation cavity is almost obliterated. Meanwhile the addition of new material in a growth region near the posterior end of the gastrula, around the blastopore, brings about an elongation of the embryo and a marked decrease in the size of the blastopore. As this elongation is more rapid

ventrally than elsewhere, the reduced blastopore is moved to a somewhat dorsal position instead of remaining strictly terminal. This more rapid elongation of the ventral side of the gastrula is a good illustration of the far-reaching *principle of unequal growth* in the process of differentiation. In fact "unequal growth," that is, unequal in quantity or rate, lies at the very foundation of many processes of morphogenesis, constituting much of the subject matter of embryology.

4. Formation of the Nervous System

One of the earliest organ systems to appear is the *nervous system*. Along the dorsal side of the gastrula, ectoderm cells begin to multiply at a greater rate than in the surrounding region, thus forming a thickened area, the *neural plate*. Further increased mitotic activity in these cells soon results in

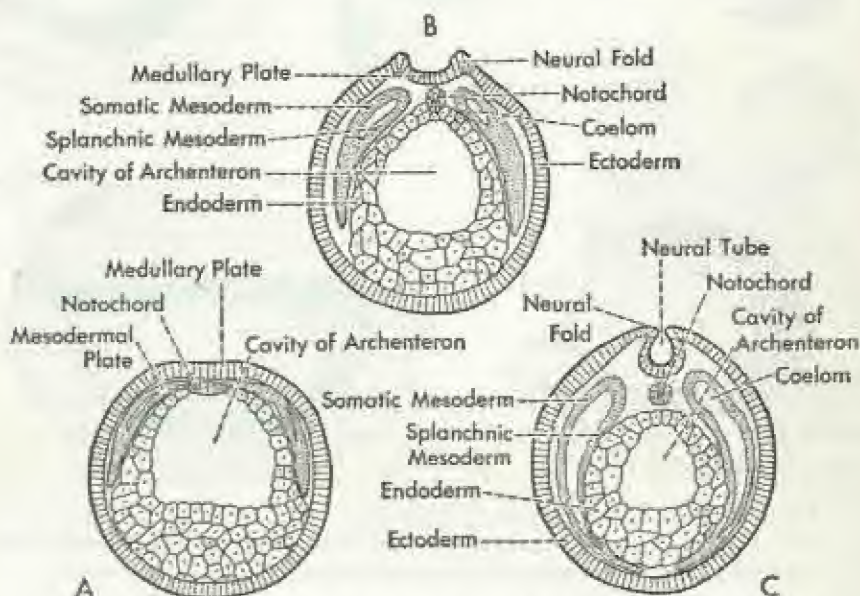


Fig. 113. Formation of the neural (medullary) plate, neural tube, mesoderm, notochord, and coelom in chordates, based on amphibians. (A, after Hertwig and Mark; B and C, after Hyman.)

the formation of a groove along the middle of the neural plate, as the cells in the mid-dorsal region push down into the underlying segmentation cavity and those on either side simultaneously are folded up into longitudinal ridges, *neural folds* (Fig. 113). The furrow between the ridges is the *neural groove*, the walls of which are the forerunner of the central nervous system. The neural folds continue to approach one another until they meet above

the invaginated groove to form the *neural tube* which soon splits off from the surface ectoderm. This process, beginning in the head region, proceeds posteriorly. Consequently when the groove has been completely closed over near its anterior end, the neural folds may be merely beginning to appear in the posterior part of the embryo. The extreme anterior end of the groove remains open for a time, however, as the *neuropore* which leads into the cavity of the neural tube, the *neurocoele*.

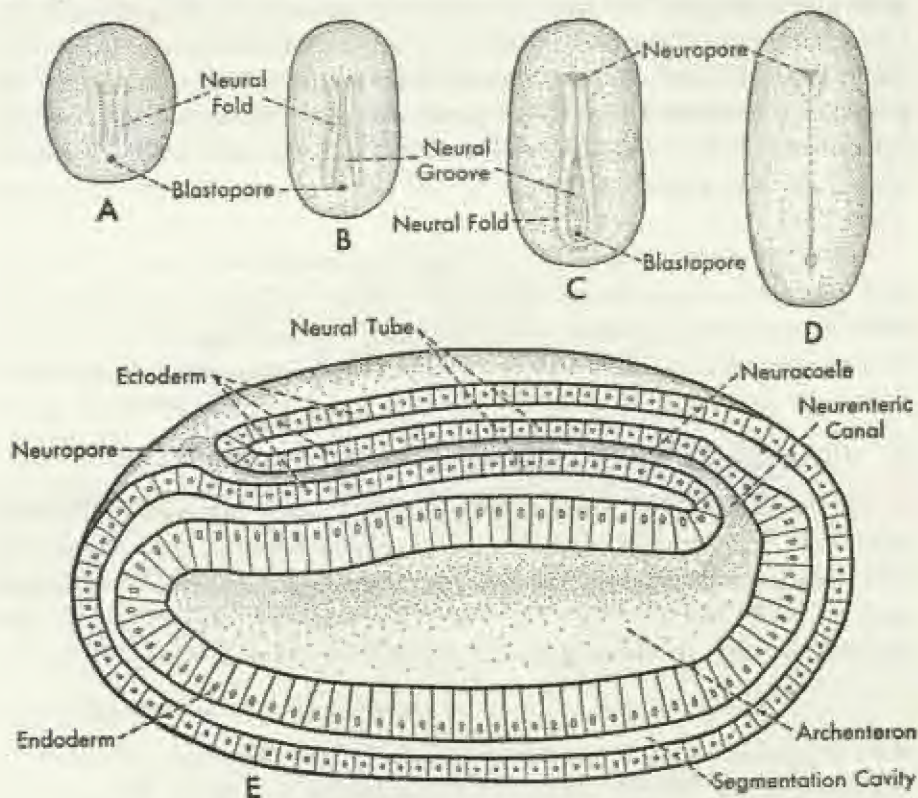


Fig. 114. Five stages in formation of neural tube and neurenteric canal. In D neural tube has closed completely except at neuropore, while anterior portion of tube has separated from superficial ectoderm; position of neurenteric canal is shown by dotted circle.

Gradually the neural folds extend farther and farther toward the posterior end of the embryo until they reach points on either side of the tiny blastopore which, as a result, then lies in the bottom of the neural groove. As soon as the two folds have extended beyond the blastopore they turn toward the mid-line where they meet (Fig. 114). As at other levels, the folds in this posterior region eventually meet over the top of the groove and

complete the formation of a tube. Because the blastopore was on the floor of the groove, there is now a passageway (*neurenteric canal*) between the neurocoele and the primitive gut cavity. This connection is later obliterated, leaving the two systems completely separate in this region.

5. Formation of Notochord and Mesoderm

Concurrently with the appearance of the central nervous system, three groups of cells grow into the dorsal part of the segmentation cavity, either from the dorsal endoderm or from the zone of proliferation just in front of the blastopore. One of these groups, lying in the mid-line, forms an unpaired strand of cells which later separates from the parent tissue to become the *notochord*. The other two groups of cells, one on each side of the notochord, are the paired beginnings of the third germ layer, the *mesoderm* (Fig. 113).

Through rapid cell proliferation these mesodermal sheets spread laterally and ventrally around the endoderm. Meanwhile each sheet has split into an outer *somatic layer*, adjacent to the ectoderm, and an inner *splanchnic layer*, next to the endoderm. The new cavity thus formed, the *coelom*, lying wholly within the mesoderm, is a single continuous space on each side of the body.

6. Differentiation of the Mesoderm

As the mesodermal sheets spread and split, each undergoes differentiation into three regions, namely: (1) a dorsal *epimere*, near the neural tube; (2) a small *mesomere*; and (3) a ventral *hypomere*, enclosing a large part of the coelomic cavity (Fig. 115). The epimere, beginning first near the anterior end, becomes gradually divided transversely into parts known

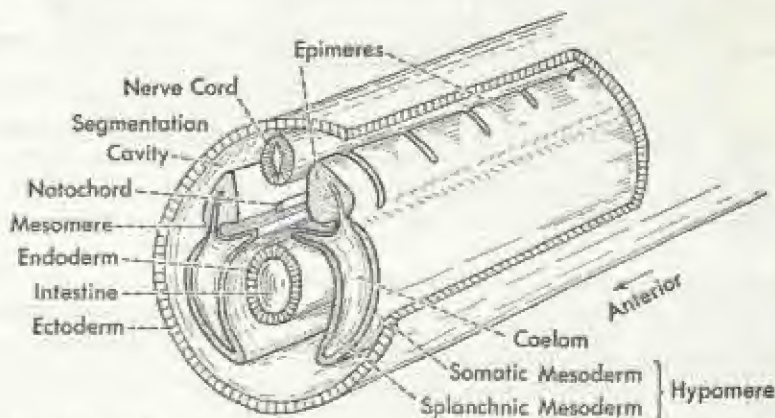


Fig. 115. Differentiation of the mesoderm in a chordate with complete cleavage.

as *somites*, which soon become separated from the mesomere. Only weak and temporary segmentation ever appears in the mesomere, while the hypomere never shows evidence of segmentation or of separation from the mesomere.

The thin-walled hypomeres of the two sides grow toward the mid-line, both dorsal and ventral to the archenteron, until they come in contact with one another to form the two-layered *dorsal* and *ventral mesenteries* (Fig. 116). Although the dorsal mesentery persists in the adult animal, nearly all of the ventral mesentery soon disappears so that the two coelomic cavities become continuous. Between the thin, approximated walls of the dorsal mesentery, blood vessels and nerves extend to and from the digestive tube.

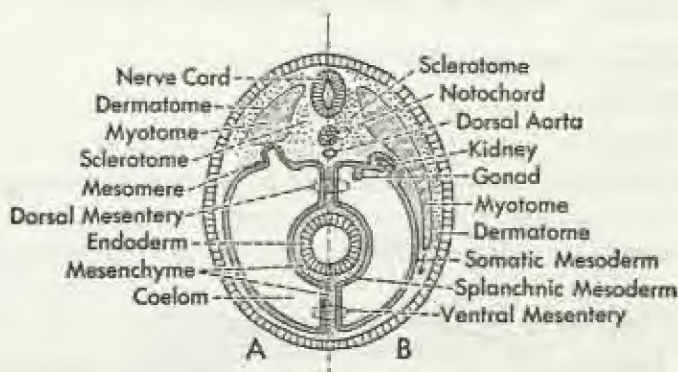


Fig. 116. Differentiation of the epimere into sclerotome, myotome, and dermatome. Sclerotome and dermatome are composed of mesenchyme. A, earlier stage; B, later stage.

7. Emigration of the Mesenchyme

From the splanchnic part of each hypomere and both portions of each epimere, cells, collectively known as *mesenchyme*, migrate into the segmentation cavity. By amoeboid movement, they may wander anywhere within this cavity. Many cells from the median part of each epimere mass alongside the notochord and nerve cord to form a *sclerotome* ("skeletal segment"), while most of those from the lateral part of the epimere gather just beneath the ectoderm as the *dermatome* ("dermal segment"). The portion of the epimere remaining after these mesenchymal cells have been given off is known as the *myotome* ("muscle segment"). See Fig. 116.

Some of the mesenchymal cells from the hypomere group about the endoderm to form the smooth muscles, blood vessels and connective tissue of the wall of the digestive tract. Other mesenchymal cells, from both hypomere and epimere, migrate throughout the segmentation cavity to form, at

appropriate places, connective tissue, cartilage, bone, smooth muscles, blood cells and blood vessels.

After mesenchymal migration has begun, the dermatomes and thin portions of the myotomes grow ventrally into the region between the somatic mesoderm of the hypomere and the ectoderm. With the filling in of dermal cells in the mid-line, both dorsally and ventrally, a continuous sheet of material, which differentiates into the derma, is laid down. Although the myotomes also grow to the mid-line, dorsal to the nerve cord and ventral to the body cavity, the muscles of the two sides of the body never fuse, but remain separated by a thin partition of connective tissue. The ventral, thin portions of the myotomes give rise to the several thin sheets of voluntary muscle tissue of the ventral and lateral parts of the body wall.

8. Assembling of the Digestive Tube

With the closing over of the blastopore, no direct opening into the archenteron remains. Later a *digestive tube*, with an inlet at one end and an outlet at the other, is established. The larger part of this food tube is made up of the archenteron, lined with endoderm, already in use. The original archenteron is supplemented at either end by ectodermal invagina-

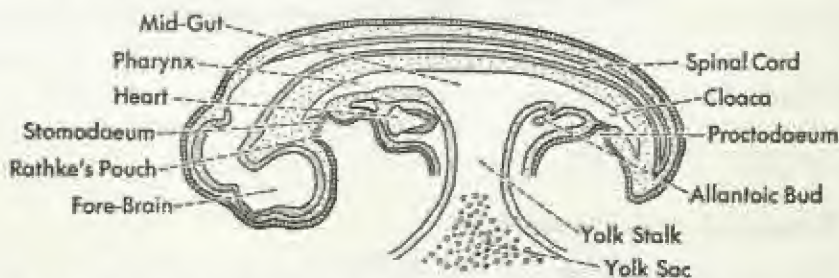


Fig. 117. Sagittal section of a four-day chick embryo. (After Patten.)

tions that come in contact with it and finally break through, thus forming a continuous canal through the body of the embryo. The inpushing of the ectoderm at the anterior end, which marks the region of the future mouth, is called the *stomodaeum*, while the corresponding invagination at the posterior end, that forms the anal exit of the food tube, is called the *proctodaeum* (Fig. 117). Thus it comes about that food passing through the alimentary tract first rubs against walls of ectodermal origin, then follows along the major distance in contact with endodermal walls where much of it is absorbed, and finally the residue passes out through ectodermal walls.

9. The Fate of the Germ Layers

With gastrulation and differentiation of the primitive germ layers there begins to be an increase in the size of the embryo, or *growth*, accompanied by diversification and establishment of the organs and systems that constitute the mechanisms of the adult animal. It is the task of *Organology*, or *Descriptive Embryology*, to follow out the changes that take place. Obviously within the confines of a brief introductory chapter it is necessary to avoid many alluring side alleys that entice one from the main highway, and to be content with a brief résumé of the structures formed by the several regions just described (Fig. 118).

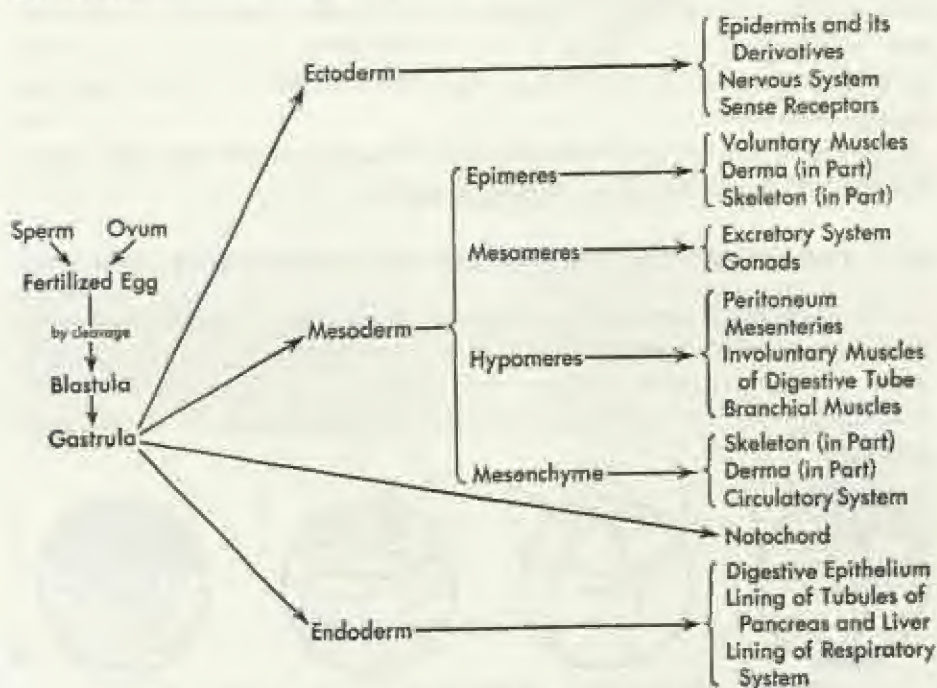


Fig. 118. The fate of the germ layers.

The *ectoderm* gives rise to: (1) the nervous system, including the brain, spinal cord, nerves, and receptor endings; (2) the lining epithelium of the mouth and nasal cavities (from stomodaeum) and of the last part of the rectum (from proctodaeum); and (3) the epidermis and all of its derivatives, including feathers, hairs, nails, claws, scales (except in fishes), integumentary glands, enamel of the teeth, and lens of the eye.

The *endoderm* forms not only the lining of almost the entire digestive

tract but also the epithelial layer in the tubules of such outpocketings of the tract as the lungs, liver, and pancreas.

Of the *mesodermal* regions the epimeres give rise to: (1) mesenchymal sclerotomes which develop into the vertebral column; (2) mesenchymal dermatomes which form most of the dermal part of the integument; (3) myotomes from which nearly all of the voluntary muscles arise; and (4) other mesenchymal cells which contribute to the formation of skeletal, dermal, and circulatory structures as well as smooth muscles.

The mesomeres are the source of the excretory system and the gonads which harbor the germ cells.

The hypomeres, in addition to forming mesenteries and linings of the body cavities, also give rise to some of the voluntary muscles of the head and neck regions and to part of the mesenchymal aggregate from which develop portions of the skeletal, dermal, and circulatory organs, and the smooth muscles.

The question of how these structures arise from their embryonic antecedents awaits our attention in later chapters.

IV. EARLY DEVELOPMENT OF TELOLECITHAL EGGS

The preceding section has concerned itself with a simplified plan of development which might be followed by an isolecithal egg of a lower vertebrate. In many respects this plan also applies to the development of telolecithal eggs but it is modified, particularly in early stages, by the presence of yolk.

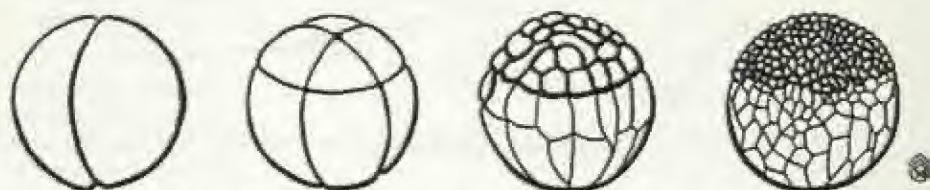


Fig. 119. Cleavage of an *Amblystoma* egg. (After Eyclesheimer.)

When the yolk is disposed polar fashion, as in an amphibian's egg, the mitoses at the embryogenic animal pole, in the neighborhood of the original nucleus, go forward at an accelerated rate, while cell division is retarded at the opposite vegetal pole where the inert yolk is particularly in evidence (Fig. 119). A *blastula* is evidently formed but the *segmentation cavity* within the hollow sphere is eccentric, its walls being of very unequal thickness, because the blastomeres at the animal pole are considerably smaller and more active than those at the opposite or vegetal pole (Fig. 120).

In reptiles and birds the results of segmentation are still further modified by the relatively enormous amount of yolk present. The nucleus of the fertilized egg undergoes the usual mitoses, but the new cell boundaries fail to be extended so as to include the great sphere of yolk material. The result is a patch or disc of crowded blastomeres of unequal size at the animal pole, the larger cells with incomplete boundaries being at the periphery (Fig. 121). Although earlier even the central cells were not separated from the yolk below, they have by this time split off leaving a space, the *segmentation cavity*, between them and the yolk (Fig. 122).

In the amphibian egg, in which the segmentation cavity has walls of unequal thickness, a slight invagination to form a groove appears on one side at the point where the upper thin wall passes over into the lower thick wall of the vegetal pole. The small cells of the upper lip (on the animal pole side) of the groove now proliferate rapidly, and the lip begins to grow down

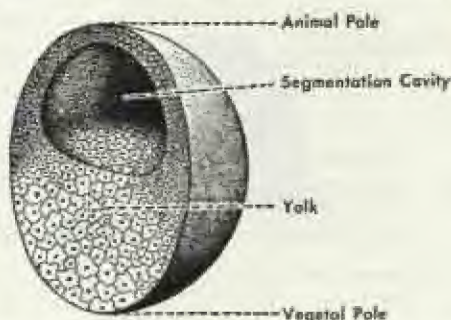


Fig. 120. A hemisected blastula of the frog. (From Huettnier, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)



Fig. 121. The segmenting disc of a hen's egg. (After Caste.)

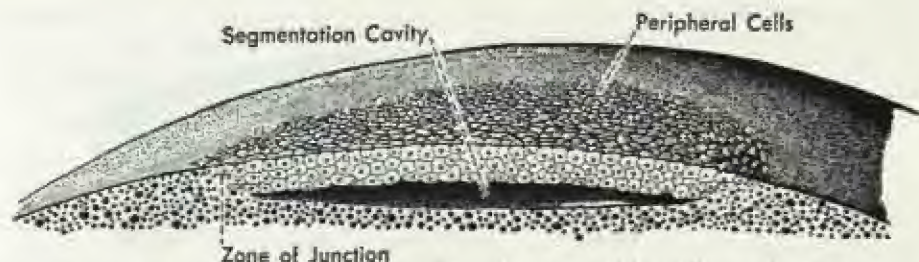


Fig. 122. Section through the blastula of a chick. (From Huettnier, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

over the large yolk-filled cells (Fig. 123). The outer layer of the lip is *ectoderm*, the inner layer *endoderm*, and the cavity between endoderm and yolk cells is the *archenteron*. Aided by some growth of the small cells over the large ones all around the equator of the blastula, the dorsal lip eventu-

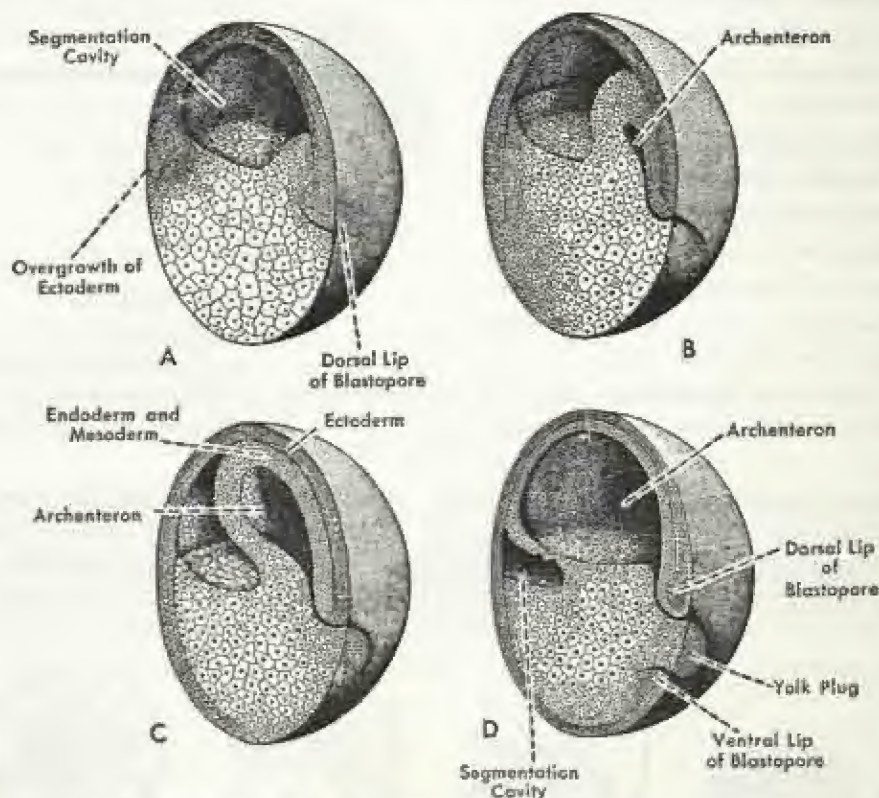


Fig. 123. Gastrulation in the development of the frog. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

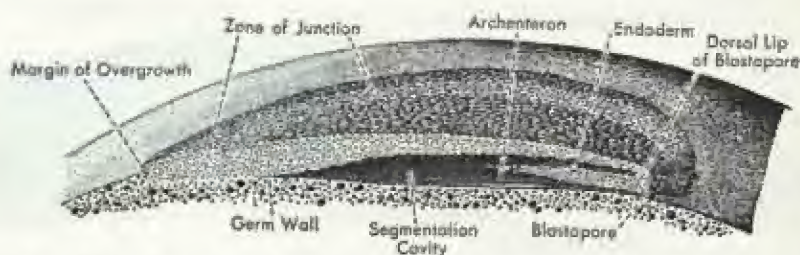


Fig. 124. Gastrula of the chick. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, copyright 1941, by permission of The Macmillan Company, publishers.)

ally covers all but a small *yolk plug*, composed of the large cells. This plug occupies what is actually the *blastopore*. Meanwhile the yolk cells themselves have been gradually shifting away from the small archenteron into

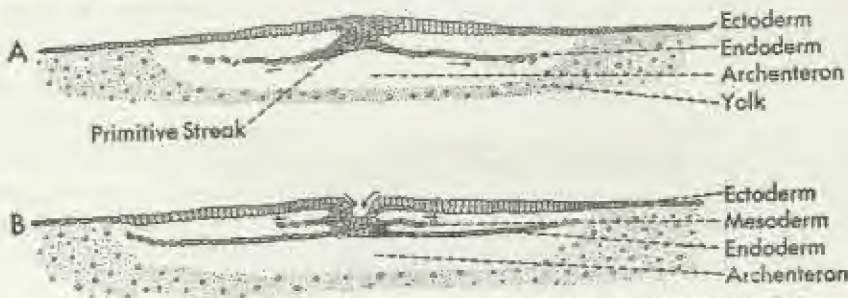


Fig. 125. Schematic transverse sections through primitive streak of the developing chick, showing formation of endoderm and then mesoderm from the streak. (After Patten.)

the segmentation cavity, with the result that the archenteron has increased considerably in size, mainly at the expense of the segmentation cavity. As this gastrulation is taking place, the *notochord* and two *mesodermal sheets* are arising from the dorsal endodermal cells and the zone of proliferation in the region of the *dorsal lip of the blastopore*. The neural tube has also been developing in a manner similar to that described above, though differing in some details. In most respects further development of the various embryonic tissues follows the general chordate plan.

In reptiles and birds, a crescentic fold of tissue forms on one side at the edge of the disc of blastomeres, sending cells underneath between the yolk and the disc (Fig. 124). The proliferation of cells, becoming most marked

in the mid-part of the fold, soon becomes evident in the disc cells in a narrow line extending forward from the edge toward the center of the disc until there is a longitudinal streak of cells, *primitive streak*, in what is really the posterior part of the now elongating disc (Figs. 125 and 126). Cells

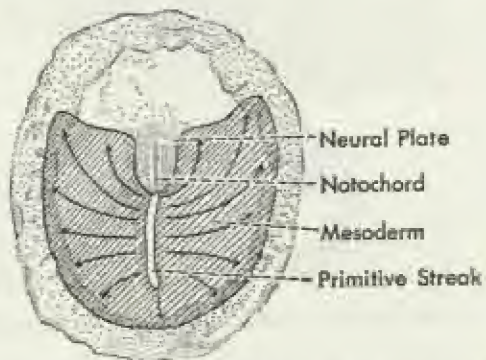


Fig. 126. Surface view of a chick embryo of about 18 hours, showing formation of mesoderm from the primitive streak region (arrows indicate direction of growth) and forward growth of the notochord from a point near the anterior end of the streak. (After Patten.)

arising in great numbers from the primitive streak are added to those derived from the infolding to form an *endodermal layer* between the yolk and those disc cells which remain on the surface as the *ectoderm*. The space between endoderm and yolk is a greatly modified *archenteron*, the floor of which is the non-cellular yolk mass.

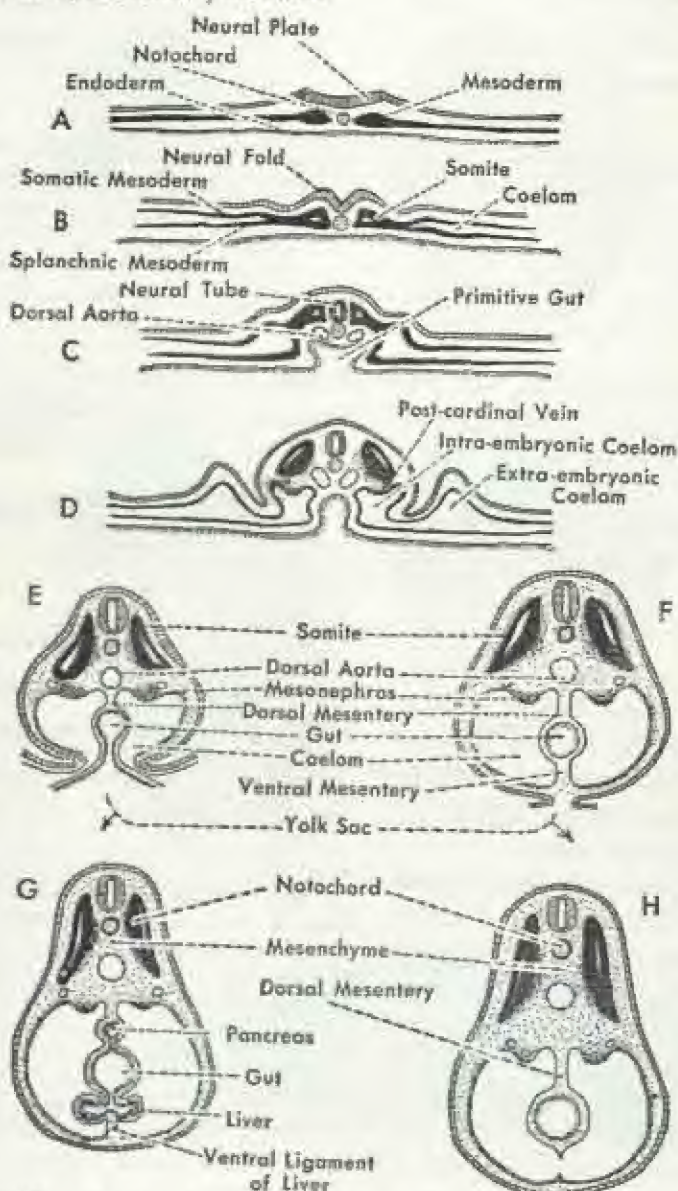


Fig. 127. A series of cross section diagrams showing differentiation of the mesoderm in the chick. (After Patten.)

Further cell proliferation from the primitive streak region gives rise to three parts: an unpaired cord of cells, the *notochord*, extending forward from the streak; paired sheets of *mesoderm*, growing laterally from the streak and spreading forward alongside the notochord. Meanwhile the ectoderm above the notochord, in front of the streak, is forming the *neural plate* and *folds* which develop into the central nervous system as in most chordates (Fig. 127).

In this manner the original patch of blastomeres on top of the big yolk mass have given rise to the nervous system, notochord, and the three germ layers. The cells on the outside have become the ectoderm, those underneath next to the yolk, the endoderm, while the mesodermal cells are proliferating between them. These pioneer cells and their descendants then set out to spread over and enwrap the entire yolk. As these layers spread out the mesoderm differentiates into epimere, mesomere, and hypomere, while mesenchyme cells appear and organize various parts in the same general manner described for most chordates.

Eventually the embryonic tissues grow entirely around and enclose the yolk in a *yolk sac*, as in a bag (Fig. 128). At the same time the embryo proper becomes raised up and separated from the yolk mass except for a slender *yolk stalk*, through which the cavity of the gut is continuous with that of the sac. Despite this continuity, the transfer of nutritive material from the sac to the embryo is apparently entirely through *vitelline blood vessels* which spread over the yolk sac with the advancing embryonic layers.

Once the three primary germ layers become established, as described above, the further development of a reptile or bird follows the general chordate plan.

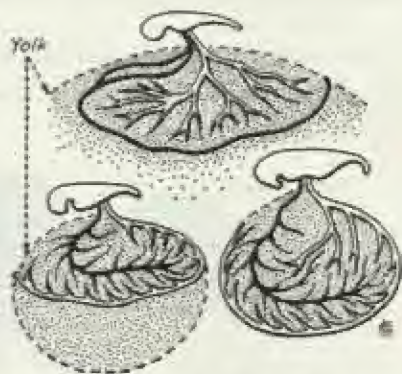


Fig. 128. Three stages in the process of enveloping the yolk by embryonic blood vessels (vitelline arteries and veins). (After von Lenhossek.)

V. EARLY DEVELOPMENT OF MAMMALS

The mammalian egg does not behave in segmentation like amphioxus, which it resembles in its small supply of yolk. The reason for the difference in development is probably that mammals have inherited developmental

traditions from a series of ancestors which amphioxus never had. In mammalian cleavage the entire egg is equally divided into blastomeres but without the regularity characteristic of amphioxus, so that, instead of a hollow blastula, an irregular solid mass of cells is formed.

Later the outer blastomeres of the germinal mass make a somewhat distinctive layer, enclosing more spherical central cells (Figs. 129 and 130).

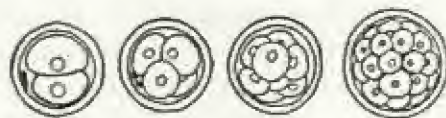


Fig. 129. Stages in the segmentation of the egg of a rabbit. (After van Beneden.)

Fluid collects within this mass and a hollow sphere results. The outer enveloping layer of cells, the *trophoblast*, comes into intimate contact with the inner wall of the uterus at the point where the developing embryo is implanted. Within the sphere

is an eccentrically located *inner cell mass*, which is destined to give rise to all the cells that are to take part directly in the formation of the embryo.

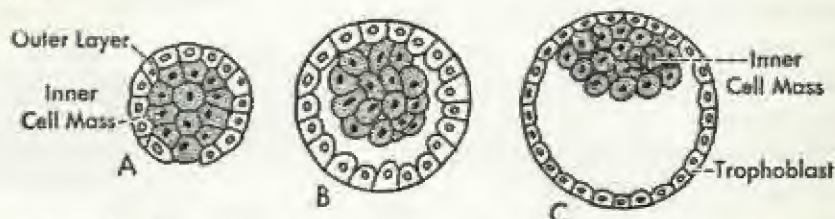


Fig. 130. Formation of trophoblast and inner cell mass in the development of a mammal. (After Keith.)

Some of the cells of the eccentric inner cell mass migrate and spread out to form a layer, the *endoderm*, lining the fluid-filled cavity (Fig. 131). This cavity now corresponds to the combined *archenteron* and cavity of the *yolk sac*, only here the entire space is filled with fluid, while in reptiles and birds there is a small liquid-filled archenteron and a large yolk-filled sac. The remaining cells of the inner mass, now the *ectoderm*, next spread out into a flat "embryonic plate" which corresponds to the ectodermal disc of the reptile or bird. The portion of the endodermal layer which is immediately beneath the "plate" belongs to the embryo proper, while the rest of this inner layer represents the yolk sac. Thus the parts present at this time may be homologized with those of the gastrula of a bird or reptile. Further development of the mammalian embryo follows, in many ways, the ancestral pattern cut out for it by the reptiles, including the appearance of a *primitive streak*, in the embryonic plate, from which cells grow out to produce *notochord* and *mesoderm* (Fig. 132).

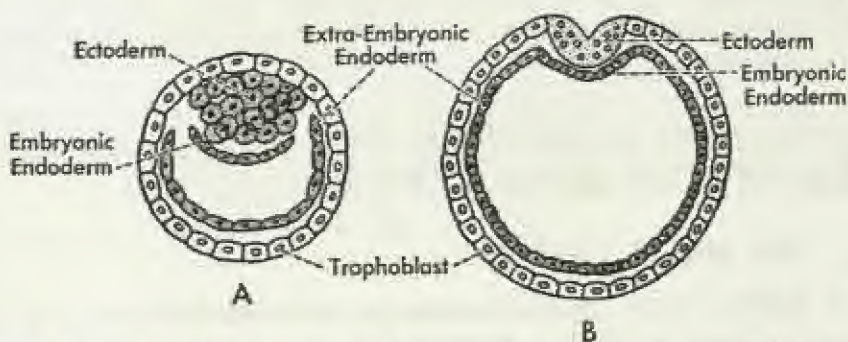


Fig. 131. Establishment of endoderm and ectoderm in mammalian development. In **A** embryonic and extra-embryonic portions of the endoderm have arisen from the inner cell mass. In **B** the ectoderm has broken through the trophoblast and begun to spread out in a layer joined peripherally to the trophoblast. (After Parker and Haswell.)

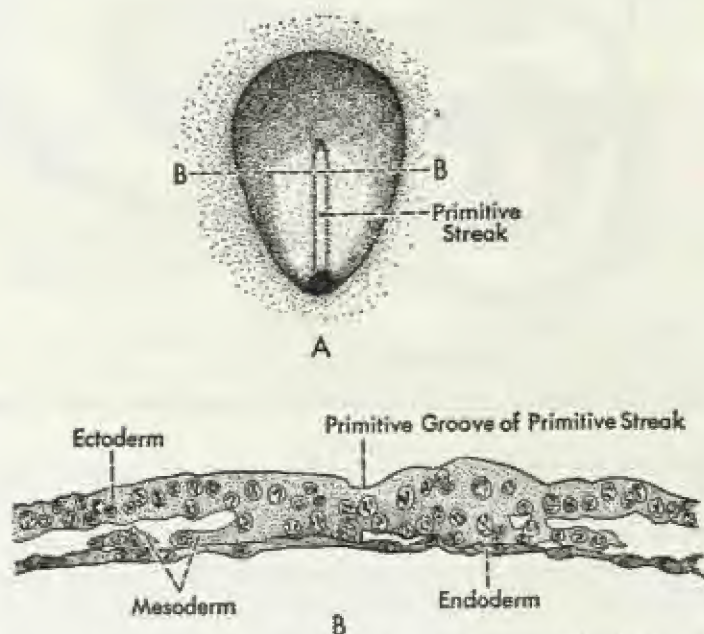


Fig. 132. The "embryonic plate," or "shield," of a rabbit of about 172 hours. **A**, surface view; **B**, transverse section at level of line **B-B** in **A**. (From Neal and Rand, *Comparative Anatomy*, copyright 1936, by permission of P. Blakiston's Son and Company, publishers. After Ascheton.)

From these few brief statements concerning the early stages in the development of various vertebrates it is clear that gastrulation and the formation of mesoderm and notochord vary considerably among the several vertebrate classes. It should be emphasized, however, that once the three primary germ layers become established they give rise to the principal organ systems with great uniformity, as shown in Figure 118.

VI. THE MAJOR CAVITIES

A coelomic cavity usually develops on each side of the body in the manner we have described, by the splitting of the mesodermal sheet. Hence it is a *schizocoele* (*schizo*, split). In amphioxus, however, the anteriormost mesoderm arises as a series of outpocketings, or pouches, from the dorso-

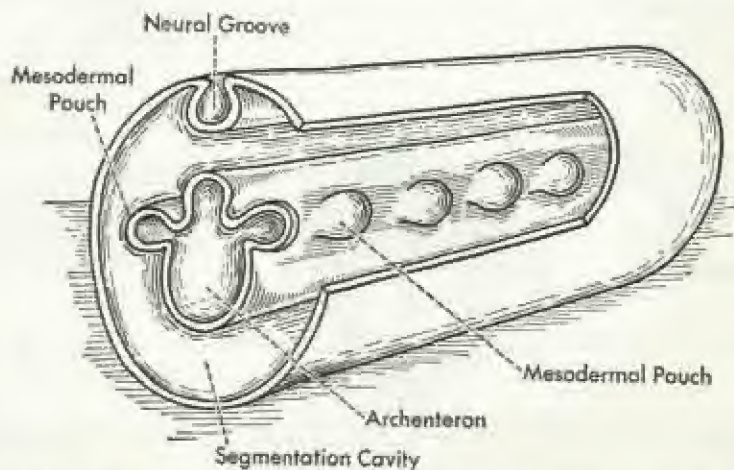


Fig. 133. Formation of mesodermal pouches in amphioxus. (After Wilder.)

lateral regions of the archenteron (Fig. 133). After the mesodermal pouches separate from the archenteron the cavities of all those on each side of the body combine to form a continuous coelom, usually known as an *enterocoele* because of its origin from the archenteron. This method of mesoderm formation does not occur in the vertebrates, with the probable exception of some amphibia, but is typical of hemichords and echinoderms. This formation of enterocoeles in echinoderms and some chordates as well as the posterior position of the blastopore in echinoderms and all chordates indicates that these two phyla may be closely related.

Mesenteries and other parts of the mesoderm arise in much the same manner whatever the method of formation of their germ layer may be. In

either case the paired coelomic cavities, confined mainly to the hypomeric region, unite into a single cavity upon the disappearance of most of the ventral mesentery. In birds and mammals the embryonic coelomic cavity becomes divided into three different sorts of spaces, namely: the *pericardial cavity* enclosing the heart, the two *pleural cavities* surrounding the lungs and the *peritoneal cavity* housing chiefly the major part of the digestive tract and the urogenital organs (Fig. 134).

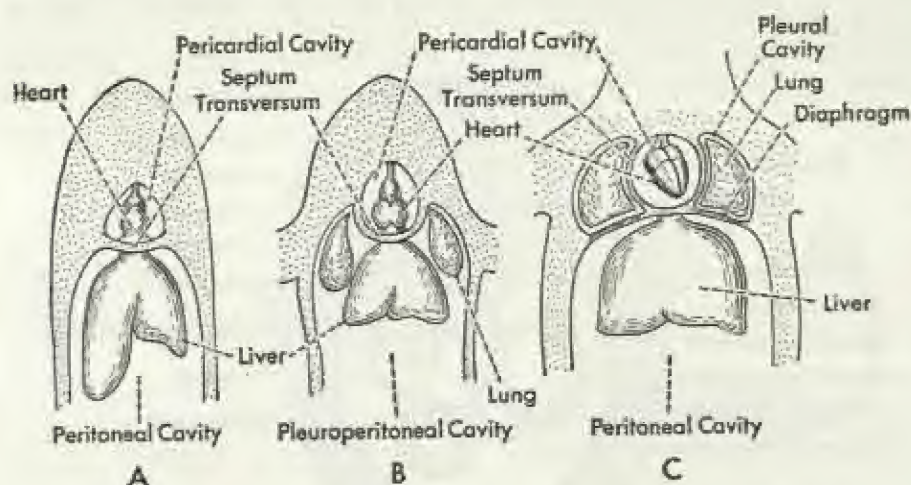


Fig. 134. Diagram showing relations of the coelomic cavities. (A), in fishes; (B), in amphibians and reptiles; (C), in mammals. (After Kingsley.)

As the first evolutionary step in lower vertebrates, the coelom becomes divided by a double transverse mesodermal wall, the *transverse septum*, into a small anterior *pericardial cavity* and a large posterior *peritoneal* or *abdominal cavity*. In some fishes (e.g. *Squalus*) this septum is not quite complete, so that a communication between the two cavities persists throughout life in the form of the so-called *pericardio-peritoneal canal* lying along the ventral side of the esophagus.

With the appearance of lungs, which grow back into the anterior part of the abdominal cavity, the name *pleuroperitoneal cavity* is more properly applied to this region of amphibia and reptiles. Usually the two lungs are in more or less individual forward extensions of the main cavity. In most of these animals the heart shifts posteriorly to lie ventral to the anterior part of the abdominal cavity, with the result that the ventral part of the transverse septum is pushed posteriorly while the dorsal part keeps its more anterior attachment.

In birds and mammals a new partition develops, extending from the ventral part of the transverse septum to the dorsal body wall. Although membranous in birds, it is invaded by myotomic muscle tissue in mammals to become the *muscular diaphragm*. In mammals the cavity anterior to this new partition is known as the *thoracic cavity*, while the one posterior to it becomes once more the *peritoneal cavity*, for the lungs are no longer included here. The thoracic cavity contains a *pericardial cavity*, ventrally in the center, and two *pleural cavities*, one on each side, lateral and dorsal to the heart.

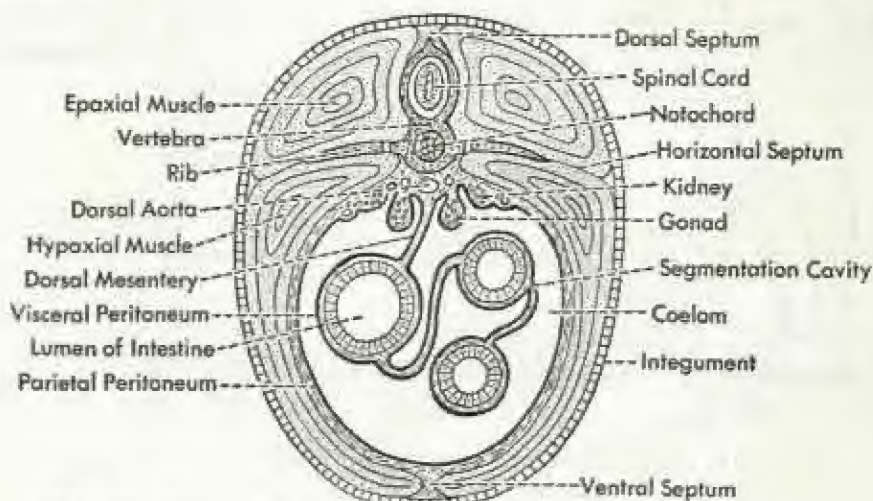


Fig. 135. Diagrammatic section through a vertebrate. (After Kingsley.)

In connection with this discussion it should be borne in mind that no organs are actually in the coelom but all, instead, are in the segmentation cavity. An organ may push into the coelom but it always carries ahead of it a fold of the peritoneal wall (Fig. 135).

VII. ORGANIZATION CENTERS

When an egg is fertilized the entering sperm is something added to it from without, starting a series of *internal changes* that finally result in the adult body. Other outside agents, like a pin-prick or contact with certain chemicals, may also, in certain cases, start up the cleavage of an egg as if it had been fertilized by a sperm. If the sequence of internal events is interrupted, or fails to occur in the nick of time, the whole subsequent procedure is upset. What is the internal mechanism that regulates this marvelous performance, once it is initiated?

It has been discovered that it is possible to transplant a bit of one embryo to an unnatural position in another embryo, and that the transplant carries out its original structural tradition even in the unnatural surroundings of its host's body. For example, the embryonic bud of a tadpole destined normally to grow into a leg, when transplanted to the back of another tadpole, will still carry out its original design and form a leg, even in so bizarre a location.

If one blastomere of a frog's egg, when it is in the two-cell stage of cleavage, is killed by stabbing the nucleus with a hot needle, the other blastomere will carry on and develop a *hemi-embryo* which may eventually restore the missing half embryo and complete the pattern of the entire embryo (Fig. 136).

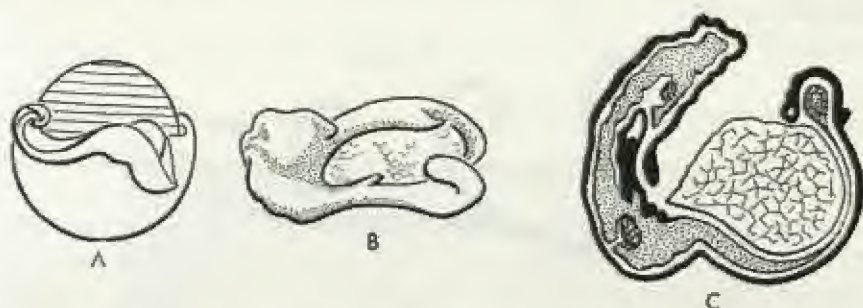


Fig. 136. Experimental hemi-embryos from frog's eggs. A, an early stage; B, a tadpole with its missing half partly restored; C, cross section of B, showing two notochords. (After Walter.)

The ability to perform such a recovery or to develop an organ from an extirpated embryonic bud lasts for only a critical brief period. Once this time is past, if the sequence of normal events is interrupted, the internal mechanism is unable to carry out the original structural design. The particular region of a developing organism that possesses this magical power of directing internal operations is called an *organization center*.

One of the earliest organization centers is around the dorsal lip of the blastopore where the mesoderm is organized. This primary center is succeeded by other formative centers, secondary, tertiary, and so on, each of which is dependent upon the successful operation of preceding centers. The discovery of such formative centers by Spemann, Harrison, and others through experiments upon developing embryos, is a promising beginning towards solving the problem of *why* the architectural plan of a particular species is carried out successfully in the innumerable individuals which grow to maturity.

VIII. SOMA AND THE GERM-LINE

In the long series of mitoses that follow the initial fertilized egg, there comes a time when the two daughter cells resulting from some particular cell division are no longer identical twins in their differentiation. They may still have the same kind of chromosomal equipment as the result of a preceding mitosis, and may be indistinguishable in appearance, but, as their future behavior shows, they have come to a fundamental parting of the ways, for one of the pair goes on as one of the ancestors of all the myriad cells that differentiate into various tissues and organs to form the growing individual (*soma*), while the other becomes the ancestor of all eggs or sperm (*germ-line*), and so is charged with the necessary business of reproducing the species.

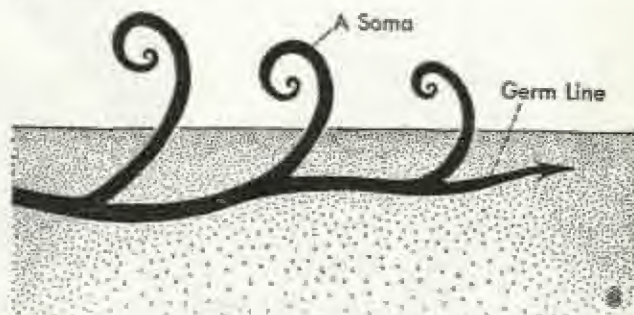


Fig. 137. Diagram to show how the continuous germ-line gives rise to successive somas, or individuals.

There are pronounced differences in these two streams of differentiating cells. The soma becomes the conspicuous thing which is known as the animal or plant body, and is biologically the guardian of the inconspicuous and less commonly known germ-line. The soma is mortal, for after a time it inevitably breaks down and dies either a natural or a violent death. The cells of the germ-line, on the other hand, although they may perish with the dying soma, are *potentially immortal*, since they form the only *biological bridge* in vertebrate animals across which the spark of life may be borne from one generation to another.

It is quite possible to go backward in imagination step by step without a break in the life-line of living cells, from any particular individual cell of an adult organism to the fertilized egg from which it came, and to see how the material in that fertilized egg was in turn a part of the unbroken series of cells of the germ-line that were housed in preceding generations of somas, and so on to the very remotest ancestral source.

The soma within limits can maintain and repair itself. The germ-line can not only do that but it can also give rise to new somas (Fig. 137). This is its mission, to reproduce new individual organisms, while it is the business of the soma, or the individual body, to nourish, protect, transport, and unite germ-lines. Otherwise inevitable death ends all.

IX. THE SUCCESSION OF GENERATIONS

The science that deals with the germ-line is *Genetics*. The resemblance everywhere so apparent between individuals of successive generations of a species has its explanation in the fact that both parent and offspring are somatic expressions of the same germ-line. That is why "pigs is pigs," and chickens hatch out of hen's eggs. The laws of heredity are fundamentally concerned, therefore, with the behavior of the germ-line and its expression in the soma.

There are various ways to get at the matter. In the past the approach to the problems of heredity has been made usually by comparing points of likeness and difference in individuals of succeeding generations of a species. This somatic method is facilitated by the experimental breeding of plants and animals. During the last forty years great advance has been made in such breeding by resort to the fundamental principles known as "Mendelism."

Another line of approach is the direct study of the germ-line, which has given rise to an increasing army of biological specialists, who are concerned with the intimate behavior of hereditary units, or *genes*, located in chromosomes, particularly those of the germ cells.

To these investigators we are indebted for an expanding body of knowledge about *spermatogenesis* and *oögenesis* in animals and plants, as well as for the facts and laws which concern germplasmal origins.

Biological Discords—Pathology

I. THE POINT OF VIEW

One of the chief concerns not only of medical practice and surgery but of daily life as well, is the repair of biological machinery that has gone wrong. Although the human machine, unlike any man-made device, has the marvelous ability to adjust the interaction of its parts and to take care of routine repairs without outside aid, there is one obvious difference between the biological and the mechanical apparatus. In the case of the human machine extra parts to replace those worn or injured, if false teeth and wooden legs are excepted, are not procurable.

Much of the success in medical practice depends upon the restorative power inherent in the patient without outside assistance, or even in spite of outside interference.

From time immemorial "medicine men" and quacks, with vendors of cure-alls and patent medicines, have thrived upon the ignorance, credulity, and fears of their victims, but there is another more reassuring side to the picture. From Hippocrates and Æsculapius down there have arisen medicine men of a different stripe who have unselfishly sought the truth about the *whence* and *why* of bodily ills, to the great advantage of mankind.

The scientific study of the *causes* underlying biological disharmonies, or disease, is the field of *Aetiology*, of comparatively recent origin. To succeed in such investigations it is necessary to know what it is that has gone wrong, and this is the concern of *Pathology* which forms the basis of every system of medicine worthy of consideration.

Pathology, or the study of the *abnormal*, goes hand in hand with *Physiology*, the science that deals with the *normal* activities of organisms. To understand the abnormal it is indispensable to first know the normal. Both physiology and pathology in turn depend upon a knowledge of *Morphology*, or the science of form and structure, since normal as well as abnormal function is referable to a structural basis.

II. DEVIATIONS FROM THE NORMAL

The "normal" is the prevailing type. If house cats with few exceptions were of the tailless Manx variety, a cat with a tail would appear abnormal, just as the unusual condition of six-fingeredness in man is regarded as abnormal simply because most people have only five digits on each hand.

Deviations from the normal frequently turn out to be a handicap to their possessors. The very fact that normality is only another way of saying that success in some particular has been gained by a *majority* of individuals, implies that variations from the standard have been less successful.

Deviations, however, are not always unfortunate. Lefthandedness, for example, is exceptional but it is not necessarily a handicap. Deviations from the normal that do handicap the possessor may take the form of deformities, misplacements, or disturbances, external as well as internal, that work ill to the organism. *Disease*, which is the particular province of pathology, may be broadly defined as *any departure from the normal standard of structure or function of a tissue or organ*.

There are at least three elementary activities of organisms, namely, (1) *formative*, that result in the growth and establishment of structural parts; (2) *metabolic*, having to do with the maintenance of the organism; and (3) *responsive*, which concern the interplay between the organism and the stimuli affecting it. Under normal conditions there is an optimum relation in each of these three lines of activity. An injury or disease may upset this optimum balance of health and well-being and cause either a cessation of these activities (death), or a quantitative or qualitative modification of one or all of them.

III. DISEASE

For centuries man's greatest obstacle to advancement has been disease. It has turned back armies and caused the downfall of empires.

In 1792 the battalions of Prussia were halted in their attack upon the French revolutionary forces by an epidemic of dysentery. Disease decimated Napoleon's horde of 500,000 soldiers, reducing their number to 3000 survivors during his march on Moscow. It was disease that reduced the crusaders from 300,000 to 20,000 in three years around 1100 A.D., while Haiti was lost to France in 1803 because yellow fever killed all but 3000 of the 25,000 soldiers sent by Napoleon to subdue the natives.

The construction of the Panama Canal was prevented until American engineers destroyed the breeding grounds of the mosquito that transmits

yellow fever. Smallpox killed more than 60,000,000 people in Europe during the 18th century and maimed many others. In Mexico, where this scourge was introduced by the Spanish, 3,000,000 Indians succumbed to it, so that the conquest of Mexico by Cortez was due to disease rather than arms. Records show that at the time of the First World War more than 150,000 soldiers and prisoners died of typhus fever during the first six months. In 1664, bubonic plague claimed 24,000 out of a population of 200,000 in Amsterdam alone.

The spectacular statistics of epidemics are hardly more appalling than the daily occurrence of preventable deaths and disabilities, happening on all sides of us, to which we have become accustomed. Future generations should be educated to appreciate the valiant attack of pathologists who seek to lessen these disasters and to alleviate human suffering and to forestall the sacrifice of lives.

IV. DISTURBANCES THAT WORK ILL

1. Internal Disturbances

Disturbances that work ill to an organism by upsetting the optimum balance may be internal or external in their origin, although it is not always easy to determine to which of the two categories a particular case belongs.

Although an outline analysis might be carried to much greater length, only four kinds of probable internal disturbances are here mentioned, namely, (1) formative disturbances; (2) mechanical interferences; (3) responsive maladjustments; and (4) hereditary handicaps.

(a) **Formative Disturbances.**—When the complicated activities of growth and differentiation, to which attention was called in Chapter VIII, are passed in review, one wonders that so few structural mistakes or accidents actually occur.

The successful outcome of all embryonic development depends constantly upon the precise timing and infallible performance of each step, because every change and advance is conditioned upon what precedes and surrounds it. In the orchestra of developing parts a group of cells or an organ that is out of rhythm, like a blundering kettle-drummer, may throw all the other performers into confusion and change a symphony into discord.

The malformations and disharmonies which result from disharmony in growth and differentiation are termed *terata*, and the somber science concerned with such morphological misfits is called *Teratology*.

Terata may involve the entire individual, as in the case of "Siamese twins" of various kinds, or affect only parts of individuals or organs, as in

such deformities as club foot, cleft palate, or hunchback. Other abnormalities may be simply groups of cells, like *tumors*, that have somehow lost step with the advancing host of correlating parts, and so fallen into disharmony. Tumors of this nature are uncoordinated members of the cellular state, and are termed *benign* or *malign*, according to the degree and manner in which they encroach upon or injure surrounding tissues. Malign tumors, like "cancers," constitute one of the most disastrous disharmonies to which mankind is subject. Much study and exhaustive research is being directed towards the understanding and control of these troublesome formative disturbances.

Under the heading of formative disturbances there should also be included modifications in growth, which are evidently associated with something wrong in the behavior of certain regulatory endocrine glands, as for example, *dwarfism* and *giantism*.

(b) **Mechanical Interferences.**—Obstructional disturbances in the nutritional mechanism or the excretory apparatus may also work ill to an organism. The circulatory system, for example, through which the individual needs of the cellular structures are supplied, may suffer from local obstructions, blood deficiency, or interference with nerve supply. When for any considerable time a part of the body is deprived of blood by hemorrhage, or by such local obstructions as may result from congestion, pressure, wounds, or blood clots, a nutritive unbalance results. If the siege is not raised eventually, local starvation and death of the isolated tissues is the outcome, or, following exposure to ubiquitous putrefactive organisms, gangrene may set in with serious consequences to the neighboring living tissues. If there is protection from such foreign invasion, and the dead tissues are not too extensive, they finally become absorbed or are sloughed off, and normal conditions are restored.

Interruptions of the stimulative service from the nerve supply, by paralysis, shock, or any other interference, are also the immediate cause of a myriad of nutritional woes.

(c) **Responsive Maladjustments.**—By responsive maladjustments are meant such functional disturbances as follow in the wake of internal disharmonies of one kind or another that interfere with physical performance. The response to overwork, for example, may cause an increase in the number of the component cells in an organ and result in *hypertrophy*, or excessive growth. If this response is called forth to meet a normal physiological emergency, as in the hypertrophy of the mammary glands during lactation, or of the uterus in pregnancy, then it is normal and lies outside the field of pathology, but if it works ill to its possessor, like hypertrophy of

the heart valves or the walls of the so-called "athlete's heart," then it becomes pathological.

Atrophy, either degeneration or arrest of growth, is an instance of nutritive disturbance that causes irregularity in the responsive activities. It usually follows a cessation of function, as when the optic nerve atrophies after the loss of an eye, or when a paralyzed leg or arm wastes away.

(*d*) **Hereditary Handicaps.**—Deviations from the normal that lead to disease may be of two kinds. First, they may be *acquired* in a great variety of ways during the lifetime of the individual; or second, they may be *germinal*, that is, inherited from ancestral streams of germplasm. Blindness, for example, may be acquired by accident any time before or after birth, or it may be germinal, as in the case of certain types of "congenital" cataract that "run in the family" and are inborn.

In the miscellaneous collection of germinal heirlooms that constitute our heritage there are bound to be some things that we wish we did not have. Every person in this imperfect world has at least one such hereditary "skeleton in the closet." Frequently the skeleton cannot be suppressed and kept concealed in a closet, but must be painfully carried about in plain sight, like the burden on the back of Bunyan's immortal pilgrim.

Diseases as such, particularly bacterial diseases, do not cross over the tenuous bridge of germ cells that connects one generation biologically with another. *Constitutions* and *tendencies*, however, that insure the eventual sequence of disease, are a part of the hereditary equipment of everyone.

The philosophy of the comparative anatomist and the pathologist consists in recognizing the fact that the most successful life does not depend upon anatomical and physiological perfection, but in making the best of imperfections.

2. External Disturbances

Many of the causes of disturbance that put the "pathos" into pathology have their origin outside of the individual in the form of various environmental factors, of which those described as (1) thermal; (2) chemical; (3) barometric; (4) mechanical; and (5) biological, are representative.

(*a*) **Thermal Factors.** Extreme variations from the normal limits of temperature to which an organism has become adapted may result in thermal disturbances that work ill. Here belong the disastrous effects of scalds, burns, and sunstrokes at one extreme, and frostbite and freezing at the other. The harm done in these disturbances may take the form of nervous shock, hemorrhage, or necrosis of the part involved, with subsequent invasion and infection by destructive bacteria.

(b) **Chemical Factors.** Injurious chemical contacts, as in the case of ptomaines and various poisons introduced into the digestive tube and the blood, cause a variety of troubles. Painters and lead-workers frequently suffer from lead poisoning. The consequences of handling phosphorus or other deleterious chemical substances are also particularly unfortunate for those who are continually engaged in their use.

(c) **Barometric Factors.** Deep-sea divers, mountain climbers, and aviators, who depart from the barometric environment to which they are normally attuned, harvest a crop of pathological protests as a result. Men in deep mines, or those engaged in tunnel construction who are forced to work for hours under abnormal atmospheric pressure, may acquire "caisson disease," which manifests itself in paralysis of the legs, profuse bleeding from the nose, ears, and mouth, or even in apoplexy.

(d) **Mechanical Factors.** Outside mechanical agencies may bring about sudden injuries of varying degrees of seriousness from mere scratches to extensive wounds that include the destruction of so much of the body as to imperil life itself. The power to repair such damage varies greatly in young and old. Comparatively undifferentiated tissues exhibit greater recuperative power than those that have attained considerable differentiation. The response of the body in repairing wounds, involving as it does the behavior of the cellular units concerned, is of particular interest to the pathologist.

Sometimes mechanical factors instead of resulting in sudden wounds, may take the form of irritants that work more slowly and insidiously. Cancer of the lip, for instance, is said to be more frequent in the case of pipe-smokers, who have subjected themselves for a considerable time to local mechanical irritation of a pipestem, than among non-smokers.

Many occupations that involve inhaling irritating dust particles, like handling coal, threshing grain, cutting stone, and polishing metals with abrasives, induce manifestation of diseases as a consequence of mechanical irritants acting upon the respiratory surfaces.

(e) **Biological Factors.** There are three general kinds of parasites that may attack other organisms and upset their normal course of living. They are (1) pathogenic bacteria; (2) pathogenic protozoans; and (3) a heterogeneous group of larger parasites, including certain worms, insects, fungi, and other harassing forms that prey upon their betters.

Pathogenic bacteria are microscopic plants that cause such diseases as tuberculosis, cholera, tetanus, anthrax, and typhoid fever. The harm they do is usually the result of *toxins*, or poisons, which they set free in the tissues of their hosts during the course of their own metabolic processes, or when they die. They may, however, by sheer force of numbers resulting from their

prodigious powers of multiplication, either plug up the capillaries in which they swarm so that the circulation of blood is impeded or prevented, as in anthrax, or they may induce the formation of a bulky mass that acts as a strangling gag upon their victim, as in diphtheria, or "membranous croup," as it was formerly called.

Beginning with Pasteur and Lister within the memory of people now living, the science of *Bacteriology*, which has to do with these minute foes of mankind, has so increased in importance and achievement that it has become indispensable in all modern medicine and surgery. Without doubt the future will see still greater triumphs and conquests in this fertile field of human endeavor.

The science of *Protozoölogy*, with its wide application to the control of diseases induced by pathogenic one-celled animals, has lagged somewhat behind the twin science of bacteriology, partly because the technic involved in obtaining pure cultures of organisms for accurate experimentation is more difficult. Nevertheless much has been learned already and greater discoveries and successes in this field surely await the investigator just around the corner.

Many diseases are connected with protozoan parasites which infest the blood of their hosts, particularly in the tropics, such as malaria and African sleeping sickness, while the troubles following in the train of amoebic dysentery are an example of the consequences caused by protozoan highwaymen that infest the digestive tract.

Parasitology in general, out of which the flourishing young sciences of bacteriology and pathogenic protozoölogy have sprung, is now usually associated with larger parasites, like tapeworms, flukes, hookworms, and other worms, that take up their domicile in the bodies of their hosts, or such external visitors as ticks, lice and fleas, which Mark Twain said keep a dog from "thinking about being a dog."

V. SOURCES OF PATHOLOGICAL KNOWLEDGE

A knowledge of the facts of pathology, that is daily contributing so much to the alleviation of abnormal conditions, is gained principally through clinics, autopsies, physiological and micropathological research, comparative pathology, and animal experimentation.

Clinics include bedside experiences gained by actual observation of the abnormal conditions exhibited by the patient.

Autopsies are post-mortem examinations in order to find out what has gone wrong with the machinery of biological clocks that have stopped.

Micropathological research is directed towards an intimate understanding of the behavior and appearance of cellular units under abnormal conditions. It includes not only *Pathological Histology*, but also *Bacteriology* and *Pathological Protozoölogy*.

Comparative Pathology, also with human pathology as an objective, gains added facts by the indirect method of approach through other members of the animal kingdom. Man is too complex a mechanism to be understood at once without some preliminary acquaintance with simpler mechanisms of animal life. Moreover, pathology in general is much more than the science of human ills. It is a field of study fertile enough to promise rewards to the student of pure science whose eyes are not necessarily fixed upon immediate utility to man.

Animal experimentation has made possible not only a knowledge of the facts and principles of pathology, but has also cleared the way for the diagnosis and control of the pathological disharmonies that beset mankind. Without recourse to animal experimentation the triumphs of modern medicine could never have come about.

It is unfortunate that the word "vivisection" in this connection has become such a bogey, for it has caused many people to remain uninformed or misinformed about a very important matter. The truth is well stated by Dr. W. W. Keen in a pamphlet entitled, *What Vivisection Has Done for Humanity* published in 1910, the concluding paragraphs of which are here quoted:

"The alleged atrocities so vividly described in antivivisection literature are fine instances of 'yellow journalism,' and the quotations from medical men are often misleading. Thus, Sir Frederick Treves, the eminent English surgeon, is quoted as an opponent of vivisection in general. In spite of a denial published seven years ago the quotation still does frequent duty. I know personally and intimately Horsley, Ferrier, Carrel, Flexner, Crile, Cushing, and others, and I do not know men who are kinder or more lovable. That they would be guilty of deliberate cruelty I would no more believe than that my own brother would have been.

"Moreover, I have seen their experiments, and can vouch personally for the fact that they give to these animals exactly the same care that I do to a human being. Were it otherwise their experiments would fail and utterly discredit them. Whenever an operation would be painful, an anesthetic is always given. This is dictated not only by humanity, but by two other valid considerations: first, long and delicate operations cannot be done properly on a struggling, fighting animal any more than they could be done on a struggling, fighting human being, and so again their experi-

ments would be failures; and second, should any one try an experiment without giving ether he would soon discover that dogs have teeth and cats have claws.

"Moreover, it will surprise many of my readers to learn that of the total number of experiments done in one year in England 97 per cent were hypodermic injections and only 3 per cent could be called painful!

"If anyone will read the report of the recent British Royal Commission on Vivisection he would find, says Lord Cromer, 'that there was not a single case of extreme and unnecessary cruelty brought forward by the Antivivisection Society which did not hopelessly break down under cross examination.'

"In view of what I have written above—and many times as much could be added—is it any wonder that I believe it to be a common-sense, a scientific, a moral, and a Christian duty to promote experimental research? To hinder it, and, still more to stop it would be a crime against the human race itself, and also against animals, which have benefited almost as much as man from these experiments.

"What do our antivivisection friends propose as a substitute? Nothing except clinical—that is, bedside—and post-mortem observations. These have been in use for two thousand years and have not given us results to be compared for a moment with the results gained by experimental research in the last fifty, or even the last twenty-five years.

"Finally, compare what the friends and foes of research have done within my own professional lifetime. The friends of research have given us antiseptic surgery and its wonderful results in every region and organ of the body; have abolished, or nearly abolished, lockjaw, blood poisoning, erysipelas, hydrophobia, yellow fever; have taught us how to make maternity almost absolutely safe; how to reduce the mortality of diphtheria and cerebrospinal meningitis to one-fourth and one-third of their former death-rate, and have saved thousands of the lower animals from their own special diseases.

"What have the foes of research done for humanity? Held meetings, called the friends of research many hard names and spread many false and misleading statements. Not one disease has been abolished, not one has had its mortality lessened, not a single human life has been saved by anything they have done. On the contrary, had they had their way, puerperal fever and other hideous diseases named above, and many others, would still be stalking through the world, slaying young and old, right and left—and the antivivisectionists would rightly be charged with this cruel result."

VI. THE CONTROL OF DISEASE

In earlier days of human ignorance, disease was regarded as due to the presence of evil spirits, and cures were supposed to be effected when these malign visitors were properly exorcised by some conjurer or medicine man. Although the conjurer in various guises still trades upon superstition and ignorance, the modern controller of disease has come to recognize that all methods of healing, almost without exception, resolve themselves simply into extensions of the natural phenomena of growth and repair that are inherent in the patient. For example, it has been found that by injecting dead cultures of the causal agents into subjects infected by a pathogenic organism, there is produced in the body fluids a substance (*opsonin*) which apparently in favorable conditions unites with the living causal pathogenic bacteria and so sensitizes them that they are readily taken up and destroyed by the *phagocytic cells* of the blood. The afflicted body, therefore, *cures itself* whenever a cure is effected, and frequently nearly all that the modern medicine man can do is to direct intelligently the efforts of the body in its task of restoring normal conditions.

Three general directions are followed in modern attempts to control disease, namely, by curative, preventive, and creative medicine.

Curative medicine, finding itself in a world of disease and disaster, sets out to heal the sick and bind up the wounds of the injured. It has assumed a colossal task and, like the Good Samaritan that it is, has gone about the business with noble devotion and increasing success.

Preventive medicine, on the other hand, seeks to forestall trouble. Diseases like smallpox are prevented by vaccination, while by means of antitoxins the poison of invading germs, like that in diphtheria, is counterbalanced and rendered innocuous. Protective immunity against disease is thus accomplished by using vaccines, antitoxins, opsonins, endocrine extracts, and other resources of the bacteriologist and physiological chemist.

Creative medicine, which at present is hardly more than a dream for the future, takes a long look ahead and attempts to prevent the abnormal with all its disastrous chain of consequences, by seeing to it that, so far as possible, only the normal are born into the world. This is the hopeful field of *Eugenics*, which seeks to lessen and prevent disease by providing an hereditary equipment that is able to maintain itself triumphantly harmonious in the face of besetting discords.

All of these lines of possible betterment must advance through the frontier of *pathology*, hence the importance of this field of biology.

PART TWO

**THE MECHANISM OF METABOLISM
AND REPRODUCTION**

A Jack of All Trades—The Integument

I. IN GENERAL

In making a study of the structures of the body it is fitting to begin with the integument because, like the wrappings around a parcel, it is the first part to be encountered in the examination of any animal. It is, however, much more than a mere wrapping encasing organs within, for it is itself an "organ," just as definitely as the liver, brain, or heart are organs.

The vertebrate integument consists of the skin and its derivatives. Exposed on its outer surface to the hazards of a varying external environment, on its inner face it abuts intimately upon a closed universe of organs bathed and permeated by blood and lymph. While acting as a protective barrier, the integument not only completely envelops the entire outside of the body, including even the surface of the eyeballs, but it also passes over continuously at the nose, mouth, anus, urinary and genital openings into a related enveloping tissue, the *mucous membrane*, which lines the internal passage-ways. Thus all the organs of the body, except the integument on the outside and the mucous membrane on the inside, are completely shut off from the outside world, as if in a closed sac with no direct opening into it. Paradoxical as it sounds, food within the digestive tract is still on the outside of the body proper.

The integument may be considered a compound organ. *Morphologically* it is compound because it is structurally double, being made up in all vertebrates of *epidermis* and *derma*, or *corium*. *Embryonically* its compound character is indicated by its derivation from two separate germ layers, namely, the *ectoderm*, from which the epidermis arises, and the *mesoderm*, from the dermatome of which the derma arises (Fig. 116).

Finally, *physiologically* the integument is also a very versatile organ, since it performs so wide a range of functions that it may be quite appropriately termed a "Jack of all trades."

II. USES OF THE INTEGUMENT

Among the various uses for which in different animals the structure of the integument is adapted, are the following: (1) protection; (2) reserve food storage; (3) heat regulation; (4) sensation; (5) excretion; (6) secretion; (7) respiration; (8) locomotion; (9) sexual selection; and (10) reproduction.

1. Protection

The skin is inevitably a protective organ. Four aspects of its protective function may be mentioned. First, it shields the animal body against *mechanical injuries* that may result from pressure, friction, or blows of various sorts. Like any other wrapper, the primary function of which is to protect the enclosed parts, the vertebrate integument is admirably adapted for this purpose, since typically it is closely woven in texture, resistant, and at the same time so pliable that it tends to "give" under mechanical stress rather than to rupture or break away. Although many of the individual cells that compose it are soft and delicate, for example in the skin stretched over the knuckles, they are crushed only by a hard blow against a solid object.

In addition to the enveloping skin itself, most animals are equipped with protective integumentary modifications, such as scales, bony plates, feathers, hair, or cushions of fat, which aid in minimizing the effects of blows or injurious contact of any kind.

Invertebrates, such as crustaceans and mollusks, are conspicuously fortified by *exoskeletons* against an unfriendly world, while turtles, armadillos, alligators, and porcupines are noteworthy instances among vertebrates of animals that go forth, like armored knights of old, well clad to resist the blows and harassments of their adversaries.

Second, the integument protects the body *against foreign substances*. Whenever skin infection from any outside source occurs, it is usually through some break, however slight, in the enveloping integument. Since the skin is practically germproof so long as it remains whole, the internal realm of the body is protected from invasion through it by foreign immigrants.

Cleaning the skin of whatever undesirable substances may stick to it is usually accelerated in the case of civilized man by the application of soap and water. However, in the absence of these aids the human skin automatically cleans itself by surface renewal. Among the unsoaped relatives of man the same result is accomplished in a variety of ways. The production of mucus over the skin of certain slippery fishes and amphibians, for example,

makes a constantly renewable jacket of slime, which in sloughing off carries foreign accretions with it. In various other ways also the outermost dead layers of the skin, with such epidermal structures as hair and feathers, are, like soiled clothes, periodically cast off. When a snake "sheds its skin," although only the outermost part of the epidermis is involved, it emerges bodily clean from the gauzy cornal envelope, which may have become besmirched.

Third, the skin protects the body tissues from *excessive loss of moisture*. This is a very important function, since in living tissues water plays a major rôle. Both terrestrial and aquatic organisms are equally dependent upon water. The protoplasm in every cell must maintain a certain degree of fluidity, otherwise it dies. The enclosed universe of the body tissues contains a considerable percentage of fluids. These tissues cannot successfully be subjected to unrestrained evaporation and still carry on the life processes. Moreover, water is the basis for all internal transport of materials, as well as being the great chemical solvent of the substances to be transported. It is also the indispensable agency by means of osmosis for transferring food substances and liquid wastes in and out of the closed body. These precious underground waters of the body are conserved very largely by means of the water-proof blanket of the integument. Its impervious character serves not only to retain the moisture within but also to keep out an unregulated amount of water in the case of submerged animals, such as fishes, whose more delicate underlying tissues would become water-soaked without such protection.

Fourth, the skin or integument acts as an organ of protection in all those animals exhibiting *protective coloration*, whereby some degree of invisibility, and consequent escape from enemies, is secured by close resemblance to the surroundings. Similarly, so-called *warning colors*, like the conspicuous black and white markings of the skunk, which serve as "hands-off" signals from its possessor, are integumental modifications, protective in function. Thus "it pays to advertise," and it is the integument that provides the most available billboards.

It is obvious too that the poisonous skin glands of toads, the eluding slipperiness of certain water animals, and the embarrassing armor and spines of several well-known vertebrates, are all integumental protective devices against the attack of enemies.

2. Reserve Storage of Food

In the deeper subcutaneous layers of the skin reserve food in the form of fat is stored to be drawn upon, like a savings bank account, in times of

need. The fat stored temporarily in the liver and in the muscles is for immediate daily use, whereas what is laid down in the subcutaneous part of the skin may be retained for weeks and months.

The manner of the irregular distribution of fat in cushions and pads forms the basis of those contours in "the outward form and feature" that have pleased the eye of the artist from time immemorial, while providing an anatomical reason for the familiar phrase, "beauty is only skin deep."

In man stored subdermal fat may constitute as much as twenty per cent of the entire weight of the body. In whales and seals it forms an extensive blanket of considerable thickness, called *blubber*, that not only serves as food storage, but also acts as a non-conducting retainer of body heat.

The characteristic sexual differences in human body form and contour are largely dependent upon the distribution and manner of the dermal fat upholstery.

3. Regulation of Heat

Heat is being constantly generated by the oxidation of tissues within the animal body. Coming more abundantly from soft parts like muscles than from hard parts like skeletal organs, it is distributed and equalized by the flowing blood which permeates nearly every part of the body, so that in "warm-blooded" animals a practically constant temperature is maintained. From such an animal heat is lost in three ways: (1) with the expired warm breath; (2) with the expelled excreta; and (3) from the skin.

Every breath of warmed air carries away a certain amount of body heat, for cold air that is drawn into the lungs is warmed at the expense of the body before it is expired.

The excreta, both urine and feces, are kept at body temperature until expulsion, when a loss of heat occurs. Probably nine-tenths of the heat loss of a warm-blooded animal like a mammal, however, is through the skin. Regulation of bodily heat consequently is very largely an integumental function.

The skin effects the regulation of the loss of heat in two ways, one physiological and the other physical. *Physiological regulation* is brought about by the expansion, or relaxation, and the contraction of the skin and the walls of the capillaries contained therein. When exposed to cold air the skin tends to contract, sometimes to the point of forming "goose flesh," with the result that the capillaries carrying the warm blood are reduced to a smaller size and buried somewhat from the surface. The amount and degree of cold to which the circulating blood is exposed is thus diminished,

and there is a lessened loss of heat. In warm air the skin relaxes, affording the capillaries, now more exposed and with walls more expanded, an opportunity to permit greater loss of heat from the blood.

Physical regulation is accomplished by the evaporation of sweat which is constantly being excreted from the mammalian skin, even though it does not always appear in visible drops. Heat is universally required for the physical process of changing a liquid into a gas. During the evaporation of sweat the necessary heat is abstracted from the body through the skin and is thus eliminated.

Loss of heat from the body is further controlled by the fact that parts of the integument, like the blubber of a whale, serve as a non-conducting blanket to hold in the generated heat, making life endurable even in icy waters. "Cold-blooded" animals do not specialize in dermal fat.

A film of oil produced by the sebaceous glands in the mammalian integument serves the same heat-retaining function. When Gertrude Ederle swam the English Channel, she was generously greased all over in order to meet the unusual thermal conditions of that famous adventure.

In birds the dissipation of bodily heat is regulated through a covering of adjustable feathers by means of which a blanket of warmed air is retained next to the skin. The thickness of this blanket of warm air can be adjusted with meticulous nicety and almost instantaneously by fluffing the feathers. Thus, an English sparrow on a hot summer's day is streamlined with its feathers hugged tight down close to the body, but in cold weather it assumes adequate underwear by fluffing out its feathers and so surrounding itself with a more generous layer of body-insulating air.

The same result is accomplished more awkwardly in the case of civilized man by means of clothing, which in reality is nothing more than extra layers of non-conducting artificial integument added to that which nature has provided. Skin and clothes in themselves are not warm. They are simply devices for retaining heat generated within. Even the finest sealskin cloak thrown over the marble shoulders of the famous statue of Venus de Medici would not warm up that attractive work of art, whatever may have been the probable temperature of the original Venus.

4. Sensation

The most universal of all the senses, the great confirmatory *sense of touch*, has its receptors located in the skin. The allied senses of pressure, temperature, and pain are also referable for the most part to integumentary nerve endings. Even the chemical senses of taste and smell, which occupy the neighboring mucous membranes of the nose and mouth cavity of higher

forms, are still found on the outside of the body in the skin of the lower aquatic vertebrates.

5. Excretion

Among mammals the sweat glands supplement the kidneys in removing waste products from the blood. The mammalian skin has been referred to quite appropriately as an "unrolled kidney," since each sweat gland in the skin, with its accompanying capillaries, is a complete kidney apparatus in miniature. Whenever the activity of the sweat glands is accelerated by exercise, heat, or diuretic and diaphoretic drugs, such as aspirin, caffeine, or pilocarpin, there is less work for the kidneys to do.

The constant shedding of corneal material from the surface of the vertebrate skin also may be regarded as a kind of excretion from the integument.

6. Secretion

The most notable example of the integument functioning as an organ of secretion is found in mammals, whose mammary glands, which are a very specialized form of the integument, develop as an indispensable part of the reproductive apparatus of these vertebrates.

There are also present in the mammalian skin, associated with hairs, a great number of sebaceous glands which secrete an oily substance that tends to spread over the skin, rendering it supple and more or less resistant to soaking by water and to loss of heat. In fishes and amphibians the mucous glands, already mentioned, are also important organs of secretion.

Other instances of the integument functioning as an organ of secretion could be cited, particularly among invertebrates, as, for example, the "crust" of the crustaceans, which is a product of the *hypodermis*, or invertebrate skin.

7. Respiration

The moist skin of the amphibians accomplishes to a remarkable degree the exchange of gases which constitutes the process of respiration. *Cutaneous arteries*, for example, supplying the skin of a frog, are larger than the *pulmonary arteries* that go to the lungs. Even in man the skin supplements the work of the lungs.

The gills of water-dwelling animals may be regarded morphologically as extensions of the skin, as are also the *tracheae*, or breathing tubes of insects.

8. Locomotion

The cilia and flagella by means of which microscopic aquatic forms move about are derivatives of the outer envelope of these skinless animals, while in the diversified group of the arthropods, which include much over half of all known kinds of animals, locomotion is accomplished by lever-like appendages, the actuating muscles of which are attached to the inside of the integumentary exoskeleton. The wings of insects are entirely integumentary.

Among vertebrates the fins of fishes and the wings and tail feathers of birds that are essential to locomotion, are also integumentary in origin. The skin takes a conspicuous part too in the wings of bats, and in the flying mechanism of all gliding animals, such as flying squirrels, flying lemurs, and the "flying dragon" (*Draco*) of India, as well as in the wings of the extinct pterodactyls, which had a web of skin stretched between the fourth finger and the sides of the body. Web-footed animals like ducks and frogs depend upon the skin between the toes to enable them to paddle in the water.

III. THE HUMAN SKIN

1. Macroscopic

The human skin as a whole conforms to the underlying parts of the body as a continuous organ. A baby, which at first may easily be held in the palms of two hands, grows in three dimensions, but the skin keeps pace with the change in size, always fitting the enlarging body perfectly without any bursting at the seams. The clothes, or adventitious skin, in which the child is encased by its parents are frequently too large, because of the hopeful expectation that he will grow to fit them eventually. Not so the marvelously pliable skin. Its smooth expanse is diversified by a few noteworthy elevations and depressions, as when it is stretched over the cartilaginous framework of the external ear, or descends into the ear passage itself. The innumerable tiny pits, appearing wherever there are emerging hairs or openings of the miniature volcano-like sweat glands, are microscopic depressions that do not entirely penetrate the skin or in any way interrupt its continuity.

Wrinkles and creases around the joints aid in accommodating the elastic integument to changing contours. In old age the skin frequently exhibits wrinkles, because it does not shrink as rapidly as the underlying muscles, in the process of diminishing repair attendant upon advancing years.

The skin is thinnest where it passes over the exposed part of the eyeball. It is so thin and translucent here, as well as in the double layer of the eyelids.

that it is possible to perceive light through three layers of skin at once, a fact easily demonstrated by turning the closed eyes toward a brilliant light, when the difference between light and darkness is distinguishable through the double skin fold that is the eyelid, and the continuous *conjunctiva* which constitutes the front face of the cornea (Fig. 717).

The thickest region of the skin is found on the soles of the feet. Corns, callouses, and other local thickenings wherever there is continued excessive friction or pressure, are evidences of increased thickness by use and are particularly pronounced on the soles of the habitually unshod.

According to Lamarck the thickened skin on the soles of a baby's feet before they have been subjected to use is inherited from ancestors who acquired it while walking up and down the earth. This is by no means, however, the most plausible explanation. Mudpuppies (*Necturus*) likewise have the thickest skin on the soles of the feet. Since these primitive amphibians have their bodies always supported by the surrounding water, they do not use the soles of their feet, nor is it likely that any of their ancestors did so. Obviously there must be another reason for the differentiation in skin thickness on the soles of the feet.

According to Rauber the *area* of a typical human skin is about 1.6 meters square, or approximately five feet square. This fact is instructive when it is remembered that certain functions of the skin, as an organ of excretion or respiration, for example, depend upon its expanse.

The weight of the human skin with the subcutaneous fat removed, as determined in autopsies, is stated by Bischoff to be 3175 grams for a thirty-two year old female, and 4850 grams for a male thirty-three years old, or approximately 7 and 10.7 pounds.

The *color* of the skin depends upon two factors, namely, translucency, which permits the underlying capillaries to show through as in blushing, and the presence of pigments, of which there are several kinds, white, yellow, black, and red. Excepting in albinos, these pigments are all present in varying proportions in the different races of mankind. They are unequal in distribution, even in a single individual, being heavier on exposed parts of the skin, and around the axillae, nipples, and genitalia. The general color of the skin of so-called white people varies also with age, from pink babyhood to yellow senescence.

Characteristic blue-gray birth marks in the sacral region of newly-born mongoloid people, which fade out in the course of two or three years, are due to brown pigment granules located in the deeper translucent layers of the skin.

Nerve endings, except those of the most undifferentiated character, do

not ordinarily extend into the intercellular spaces of the epidermis. Consequently stimuli which affect the body must reach the deeper-lying nerve endings of the corium *through* the protective barrier of the epidermis.

2. Microscopic

The cells of the epidermis are arranged in stratified layers, like the leaves of a book, with the most important and indispensable layer next to the corium. From it the other, more superficial, layers are derived, together with such accompanying modifications as hair, feathers, and nails. This remarkable life-giving restorative layer of germinative cells is called the *Malpighian layer* (Fig. 138), in honor of Marcello Malpighi (1628–1694) who first pointed out its significance, thereby erecting to his name a memorial far more enduring than an isolated mausoleum or a marble shaft.

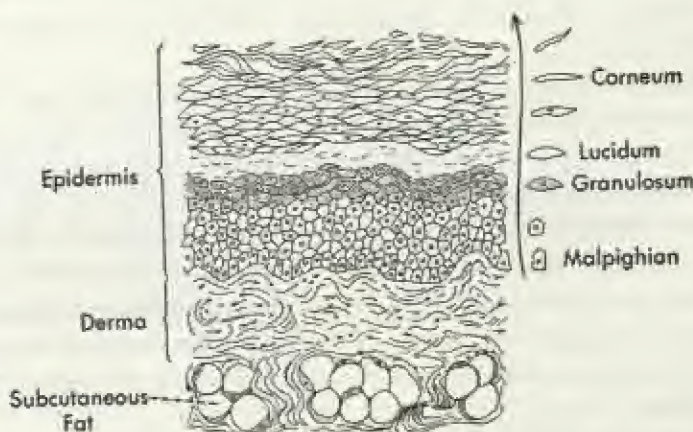


Fig. 138. Diagram of the skin, showing how the Malpighian layer gives rise to the superimposed layers of the epidermis. If drawn in proportion, the derma would be several times as thick as the epidermis.

The cell progeny arising from the germinative Malpighian layer are gradually modified while they are being crowded toward the exposed surface of the skin. Their walls become thicker at the expense of the cytoplasm, while the breakdown of their nuclei is accompanied by a sequence of chemical changes in the cell substance. Finally, each cell flattens until eventually only a dead scalelike remnant remains, like the collapsed skin of a grape after the pulp has been squeezed out. The squamous husks of the outermost dead cells thus formed are constantly breaking free from the underlying layers, being shed with no interruption of function of the skin as a whole, while at the same time a continuous renewal from the Malpighian layer

below is maintained. Dandruff is formed of the matted masses of the outermost dead epidermal cells.

It has been estimated that a person who has attained three score years and ten has, quite unawares and painlessly, gotten rid of over forty-five pounds of dead and discarded epidermal cells. Due to the eternal youth of the Malpighian layer, the skin in this way is cleaned over and over without wearing thin the way clothes do that are repeatedly scrubbed. The dead outermost layer is the *corneum*. The region between the outer corneum and the living Malpighian cells below is characterized in certain areas of the human body by the presence of two transitional layers, called the *stratum granulosum* and the *stratum lucidum*. The former is best seen in cross sections of skin taken from the soles of the feet or the palms of the hands. It is several cells in thickness next to the Malpighian layer, and is called "granulosum" because, upon the breakdown of the Malpighian nuclei, *kerato-hyalin* granules (Waldeyer) are formed, which give it an appearance of greater density.

The apparently homogenous stratum lucidum, which lies just outside the stratum granulosum and is derived from it, owes its semi-transparency and comparative resistance to all ordinary histological stains to the fact that the kerato-hyalin of the stratum granulosum becomes changed at this point into a different chemical compound, called *eleidin* (Ranvier). This layer is usually wanting except where the skin is particularly thick, but it reaches a conspicuous development in the nails, which it principally composes.

Skin pigment is usually located in the Malpighian layer of the epidermis, although in some vertebrates it is distributed among the deeper-lying cells of the corium.

The *corium*, or *derma*, is the distinctive part of the vertebrate skin, being unrepresented in invertebrate integuments. It is a network of connective tissues, consisting of cells and fibers produced by cells, felted together. It underlies the superficial epidermis and is many times thicker. When leather is made it is the corium that is tanned to produce it, the epidermis being discarded. The corium of the human skin as well as that of different animals can be made into excellent leather. As a matter of historical fact, during the French Revolution, shoes were made from the tanned skin of guillotined persons. It is related of one Johann Ziska, a fire-eating German patriot of olden days, that he stipulated in his will that his skin be tanned and made into a drumhead, the martial resonance of which should incite those who heard it to fight as valiantly as if his own voice were urging them on.

Among the many structures embedded in the corium are: capillaries and lymph vessels in abundance, nerve endings, sense organs, migrating

pigment cells, deposits of glycogen and fat, smooth muscle cells, sweat glands, sebaceous glands, and hairs, the last three being downgrowths from the epidermis.

The deeper parts of the corium form the *subcutaneous layer*, characterized by the inclusion of masses of soft fat cells and by the looser weave of the felted reticulum, which allows greater freedom of motion to the underlying muscles. Its blood supply may include a large fraction of the total amount of blood in the entire body. Some of the fibers of the subcutaneous region interlace with the fibers composing the connective tissue sheaths that envelop the muscles, thus fastening the skin down, as it were, more firmly. This is demonstrated better in the palm than over the back of the hand where the skin is looser.

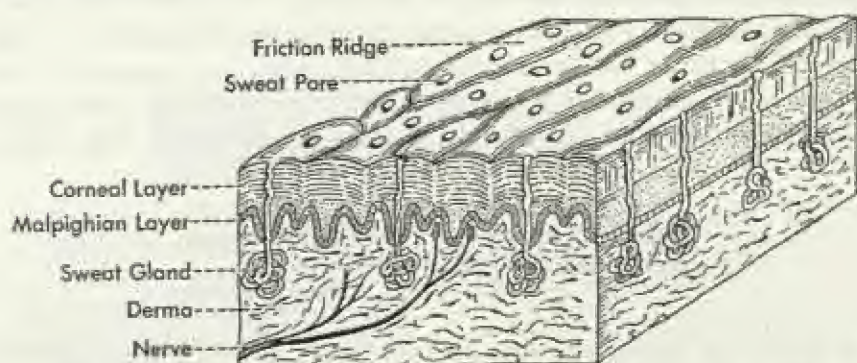


Fig. 139. Diagram showing some of the details of friction skin. The ridges on the surface, matched by corresponding epidermal projections into the derma, are penetrated by the ducts of the sweat glands which lie coiled up in the derma below. Two sensory papillae are shown. (After Wilder and Wentworth.)

In regions of the body such as the finger tips that are much in contact with things, the outer part of the corium just under the epidermis is thrown up into rows of tiny projections, or *papillae*, that form ridges (Fig. 139). It is customary consequently to speak of a *papillary layer* of the corium, although stratification of the corium is not as pronounced as stratification of the epidermis. The roughened papillary layer helps possibly to hold the corium and epidermis together at points on the skin where friction or pressure is frequently applied, for the epidermis dovetails intimately into the minute hills and valleys formed by the dermal papillae.

There are two sorts of papillae in the papillary layer, namely, *nutritive* and *sensory*, the former containing a capillary knot, the latter occupied by a sensory nerve ending. It is possible to demonstrate these two kinds of

papillae experimentally in the finger tips by patient manipulation with a very fine needle. When a nutritive papilla is punctured there is no particular pain, although a tiny drop of blood may appear, but when a sensory papilla is pricked no blood flows and pain is felt. Both kinds are so close together, and any needle point is relatively so large, that it requires nice discrimination to perform the experiment successfully.

Wherever papillae are present, three layers, which shade imperceptibly into each other, may be distinguished in the corium, namely, *papillary*, *reticular*, and *subcutaneous*.

3. Embryonic

As already indicated, the human skin as well as the vertebrate skin in general has a double embryonic origin. The epidermis, which is the primary component, arises from that part of the ectoderm remaining after the medullary tube, which forms the central nervous system, has migrated in from the outside by invagination. It consists at first of a single layer of ectodermal cells that soon gives rise to a temporary skin, the *epitrichium* (Fig. 140), a



Fig. 140. Skin from the head of a human embryo of 2½ months. (From Bremer and Weatherford, *Lewis and Stöhr's Histology*, copyright 1944, by permission of P. Blakiston's Son and Company, publishers. After Bowen.)

delicate outer layer of somewhat swollen cells which take certain stains distinctively, thus showing a specific chemical character. Corneal cells, derived from the Malpighian layer, soon appear under the epitrichium until, at the age of about three months in the human embryo, the epidermis of the fetus has acquired a thickness of three or four cells deep. About the fifth month of fetal life, when embryonic hairs begin to emerge from the skin, the gauzy epitrichium is shed from the entire body, excepting the palms and soles, into the amniotic fluid, and is never replaced in kind. The name *epitrichium* (*epi*, upon; *trichium*, hair) signifies that this layer temporarily rests upon the tips of the budding hairs. A more inclusive term for this evanescent embryonic mantle is *periderm* (*peri*, around; *derm*, skin), since it is present as a part of the embryonic skin of reptiles and birds also, where there are no hairs upon which it can rest.

The corium is derived from cells of the somatic mesoderm and the mes-

enchyme. It is secondarily wedded to the overlying epidermis, which it eventually exceeds many times in thickness.

IV. COMPARATIVE ANATOMY OF THE INTEGUMENT

1. Invertebrate Integuments

The microscopic bodies of protozoans are without a true integument, although in *Amoeba* there is a clearer marginal area, the *ectosarc*, which is different from the more granular inner part, or *endosarc* of the cell.

In other invertebrates that expose a cellular covering to the outside world, the integument is entirely *ectodermal* in origin, the mesodermal component being absent. No one has ever heard of leather being made from any backboneless animal, for leather is manufactured from the mesodermal part of vertebrate skin, and there is no such thing as invertebrate corium.

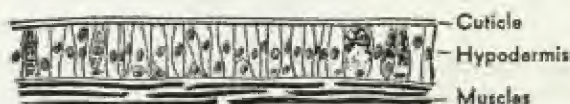


Fig. 141. A section through the integument of an earthworm. The cuticle is a secretion of the hypodermis. (After Schneider.)

The simple invertebrate skin is called *hypodermis*, in distinction to the epidermis and corium of the compound vertebrate skin. The hypodermis may consist of a single layer of *flat epithelial cells*, as in sponges and many coelenterates; of *columnar epithelium*, as in worms generally (Fig. 141); or of *ciliated epithelium*, as in flatworms and various larvae. Sensory and gland cells of various kinds may be interspersed between other cells of the hypodermis, and thus be in a favorable position to come into relation with the environment.

Frequently the hypodermis secretes a more resistant outer coat of chitin, lime, or other substance, that is not in itself cellular but which comes to constitute an integumental exoskeleton. This is particularly the case with arthropods and mollusks. As the body increases in size within the unyielding integumentary armor, it becomes necessary periodically for the hypodermis to loosen, and to cast off the lifeless, unaccommodating secreted envelope in order to renew it on a larger scale. Reminders of this process of *ecdysis*, or "molting the skin," which is typical of arthropods particularly during the growing stages of metamorphosis, still persist even among vertebrates in the various ways by which dead corneal cells are sloughed off from the epidermis.

Unlike arthropods, most mollusks do not undergo general ecdysis but retain, with unfortunate parsimony, the exoskeletal limy shells secreted by the hypodermis, until they become so weighted down by adding layer after

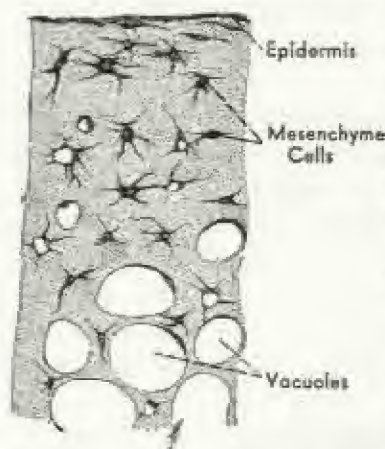


Fig. 142. Section through the mantle of a tunicate, *Phallusia*. The wandering mesenchyme cells secrete the intercellular tunicin. (After O. Hertwig.)

layer that locomotion is made difficult and sensation largely superfluous. Eventually sedentary contentment and accompanying degeneration take the place of the natural progressive evolutionary consequences that follow upon a more active and exploratory existence.

2. Tunicates

Among tunicates or ascidians, which occupy a borderland position between invertebrates and vertebrates, the epidermis is much like the hypodermis of lower forms, because of its power to secrete an external tunic of non-cellular material (Fig. 142). The peculiar substance secreted is called *tunicin*, which is not encountered elsewhere in the animal kingdom, although a chemically similar substance, *cellulose*, is a widespread constituent of plant tissues. Not only blood vessels and nerves but wandering irregular mesenchyme cells also penetrate into the tunicin matrix thus secreted, adding to the protective toughness of the mantle or tunic which gives these animals their general name of "tunicates."

3. Amphioxus

In amphioxus the typical compound integument of the vertebrates is reduced to its simplest expression. The epidermis consists of a single layer of columnar cells, which in the larval stage are ciliated as in certain worms, and which later produce a thin non-cellular cuticle that is reminiscent at least of the exoskeletal structures secreted by the hypodermis of invertebrate forebears. Thus amphioxus, in assuming the dignity of a vertebrate, does not entirely burn all its invertebrate bridges behind itself. The corium in the skin of amphioxus is represented by a thin layer of gelatinous connective tissue overlying the musculature (Fig. 143).

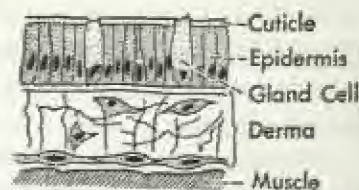


Fig. 143. A section through the integument of amphioxus. (After Haller.)

4. Cyclostomes

The slippery lampreys and hagfishes specialize in a highly glandular skin (Fig. 144). There are no scales present to restrict or modify the abundant

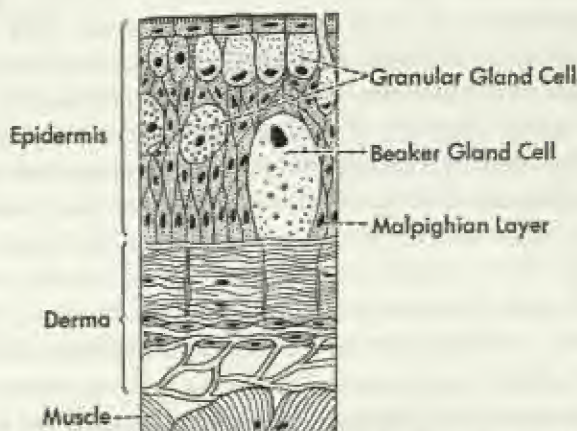


Fig. 144. Diagrammatic section through the integument of a lamprey cell, *Petromyzon*. (After Haller.)

and characteristic glands of various kinds, principally mucous, that are distributed among the cells of the thick many-layered epidermis. Epidermal cells in the skin of cyclostomes, from the deep-lying germinative Malpighian region to the surface, do not exhibit the same sort of progressive degeneration toward a lifeless corneal condition that is characteristic of the mammalian skin. The outermost cells even retain their youthful cytoplasmic character and are active enough to secrete a thin cuticle over their exposed surfaces, a lingering trace perhaps of long-vanished invertebrate days.

The horny teeth (Fig. 145), upon the surface of the pistonlike fleshy tongue and the wall of the buccal funnel, are the only epidermal cornifications in these animals. Periodically shed and renewed in the orthodox fashion of other corneal structures, they are thus to be regarded as corneal modifications of the epidermis.

The corium, which is thinner than the epidermis in these primitive aber-

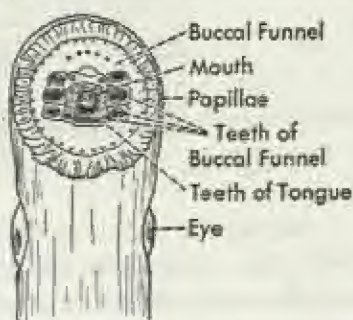


Fig. 145. Ventral view of head of *Petromyzon*, showing oral sucker with horny "teeth" and piston-like "tongue." (After Parker.)

rant fishes, is an interwoven network of vertical and horizontal connective tissue fibers, practically undifferentiated into strata.

5. Amphibians

The amphibian skin has much in common with that of cyclostomes, being highly glandular, scaleless, and with a relatively thin corium (Fig. 146). The epidermis, although consisting of several layers, is nevertheless thinner than that of cyclostomes. The glands, however, are of a more complicated type, being composed of several cells each, instead of a single cell as in cyclostomes. Although arising in the Malpighian layer of the epidermis, the compound integumental glands of amphibians do not remain in an epidermal position, as do the skin glands of cyclostomes, but push deeper down into the corium. Since amphibians are transitional animals, in and out of a water habitat, their plentiful glands help to keep the skin moist and sufficiently permeable for respiratory service. The vascularization of the amphibian skin is particularly pronounced during the critical period of metamorphosis, when, in some cases, the unusual vertebrate condition of penetration of the epidermis by capillaries takes place.

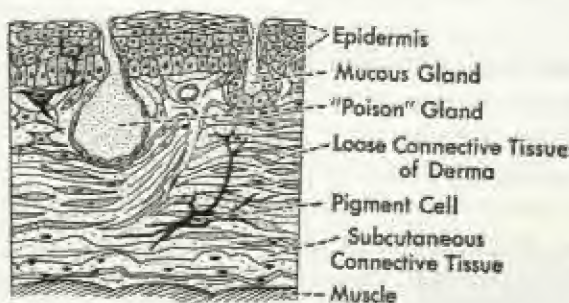


Fig. 146. Section through the integument of a frog. (After Haller.)

Among the higher amphibians which spend much of their time out of water, the corneum is differentiated in the epidermis with the result that ecdysis occurs, the dead outer layer sloughing off, sometimes in fragmentary rags and tatters. The corneum, however, is especially characteristic of land animals, not being as evident in aquatic forms.

A secreted invertebrate-like cuticle, such as amphioxus and cyclostomes have, is transiently present in some larval amphibians, much to the delight of the comparative anatomist, although it no longer appears in adult forms.

Pigment cells of the amphibian skin are located mostly in the corium, where they come under the control of the nervous system so that certain species, tree frogs for example, are able to adapt themselves with consider-

able success to the color of the background on which they find themselves, thus escaping detection. It should be noted that the skin glands of "warty" toads take on an irritating or even poisonous function, which discourages the advances of molesting enemies.

6. Scaly Forms

In many vertebrate species *scales* form a conspicuous modification of the integument. The character of the different kinds of scales will be considered later. In this connection attention will be directed simply to some of the characteristic integumental features of vertebrates with scaly skins.

Most fishes possess scaly skins. Aside from scales the integument of fishes is generally marked by the snugness with which it fits the underlying muscles. There is a tailored nicety about the skin of a fish that is not apparent in the baggy jacket of a frog, the loose integument of a bird, or the comfortable elasticity and wrinkles of the mammalian skin.



Fig. 147. Long section through the skin of a teleost, *Barbus*. (After Maurer.)

The epidermis of fishes is highly glandular. Usually the epidermal glands are superficial one-celled structures outside the scales (Fig. 147), which serve to anoint the body with mucus. Although prophetic indications of a corneum are found in some instances among fishes, in general the epidermis, as in cyclostomes, does not differentiate a definite external corneal layer, for a dead corneum is an adaptation to life on land and exposure to dry air.

The corium of fishes is a typical meshwork of connective tissue, more stratified in its deeper parts, and bearing the embedded scales to which it gives rise. Frequently the corium as well as the epidermis displays pigment of different kinds that decorates the body with an endless variety of patterns and colors, particularly in brilliant bizarre tropical fishes.

In the evolution of *amphibians* it appears that multicellular glands have displaced scales as the most characteristic features of the skin. These two structures are to a considerable degree mutually exclusive. A truly glandular skin would be hampered by the presence of scales, while a scaly skin is in no wise a convenient place for glands. The tiny one-celled mucous glands

over the surface of the scales of a fish are not to be compared in this connection with the dominant many-celled glands that characterize the amphibian skin.

Extinct stegocephals of the Carboniferous Age were as scaly as any of their contemporary fishlike neighbors. Many of them were large creatures resembling salamanders in form though greater in size (Fig. 29). They were conspicuously clothed with a cumbrous plate-like armor quite in style, for they lived in the days of scales when defensive knighthood was in flower among the animals of the earth.



Fig. 148. Section through the skin of a caecilian amphibian, *Ichthyophis*. The scales, embedded in the corium, are in black, between two giant gland cells. Two smaller epidermal glands projecting into the corium, are represented near the surface. (After P. & F. Sarasin.)

Of modern amphibians only the degenerate tropical caecilians (Gymnophiona) have any suggestive trace of scalliness. The cylindrical bodies of these small wormlike animals are encircled by bands of tiny scales embedded in the skin, alternating with areas of a typically glandular character (Fig. 148). In the skin of these lowly inconspicuous bearers of the amphibian name, is written the final episode of the evolutionary story of the rout of scales by glands.

The high water mark in completeness and elaboration of a scaly skin is reached by *reptiles*. One has only to examine with care the pattern, sculpture, and arrangement of the scales on a snake or a lizard, to be impressed with their exquisite perfection.

As a group, reptiles are definitely committed to life on land, in spite of certain backsliding exceptions. This fact has left its modifying impress on the skin, which is no longer thin, moist, and respiratory, but thick and cornified against exposure to dry air. The struggle for a place in the sun between scales and glands has had quite a different issue in reptiles than in amphibians, since the former habitually rub much against the dry ground, thus having use for a corneal skin to safeguard them against frictional contact as well as desiccation in dry air. In consequence ecdysis is necessary for the removal of the dead outer layer of epidermis. Integumentary glands, which are superfluous in a highly cornified skin, are found only in exceptional cases as relics of the days before the ascendancy of scales.

Some extinct reptiles, for example ichthyosaurs and pterodactyls, apparently had a scaleless skin, but most of the dinosaurs and their mesozoic relatives were burdened with an enormously developed integumentary armor

made up of large dermal plates (Fig. 36D), which were usually embossed in *bas relief*, and sometimes bore along the back formidable spines projecting upward two feet or more.

The corium in modern reptiles plays a secondary rôle, while the epidermis reaches perhaps a greater elaboration than in any other group of vertebrates.

Among *birds* and *mammals* scaliness is of exceptional occurrence. The scaly legs and feet of feathered birds (Fig. 149) reveal their reptilian ancestry, while there are a few scale-specialists among mammals.

7. Birds

Anyone who has ever attempted taxidermy knows how loose, thin, and easily torn is the skin of a bird. Those parts not covered by feathers, like the shanks and the bare areas around the base of the beak, exhibit a thickened corneal layer of epidermis, but everywhere else not only the epidermis but also the corium is reduced to a delicate thinness.



Fig. 150. Embryo of *Erinaceus*, the European hedgehog, 4.5 cm in length, showing a temporarily scaly skin. (After Haeckel.)



Fig. 149. Scaly foot of an osprey. (After Schöff.)

The typical looseness of a bird's skin, so unlike the tightly fitting integument of the fishes, is an advantage in flight, enabling the muscles, unhampered by a binding integumentary covering, to contract freely and to change their shape easily. The looseness of the skin on the belly of penguins serves a special purpose adapted to icy antarctic conditions. During incubation the single egg is lifted off the frozen ground to a secure position on top of the webbed feet of the parent bird and a generous apron of loose skin from the region of the belly is snugly wrapped around the egg to keep it warm.

Exoskeletal structures of birds, such as feathers, beaks, leg-scales and claws, are entirely epidermal, since dermal elements like the scales of fishes or the bony plates of certain reptiles are absent in this group.

8. Mammals

Among the few cases of real scaliness in mammals are the armored armadillos of America and the pangolins or scaly anteaters of Africa. The skin of the fetal brown bear and European hedgehog (Fig.

150) too are scaly all over with hairs interspersed. Rats, opossums, and beavers have scaly tails that are conspicuous emblems of ancient allegiances which the comparative anatomist who runs may read.

The essential features of the mammalian integument have already been described in the previous section on the human skin. It may be emphasized here, however, that among mammals the corium reaches its greatest development, becoming many times thicker than the epidermis.

The conspicuous modifications of the mammalian epidermis are hairs and glands. These structures with others will be considered in the next section.

V. DERIVATIVES OF THE INTEGUMENT

1. Glands

(a) **In General.**—Glands are cellular structures that produce either a secretion or an excretion. In addition to the integumentary glands considered in this chapter, there are other glands that open on the mucous membranes lining the internal passage-ways, and still others within the body which, in consequence of having lost their ducts, depend upon blood vessels for the disposal of their products.

All of the integumentary glands of vertebrates take their origin in the Malpighian layer of the epidermis. They may consist of single cells which have gone farther than their ectodermal neighbors in glandular specialization, or they may be composed of groups of similar cells that join in the common enterprise of producing some kind of substance which is, or is not, of use to the organism. In the former case it is a secretion, and in the latter, an excretion.

Glands such as the sebaceous hair glands are called *holocrine* because in the production of secretions individual cells are used up, extruded with their secretions, and replaced by new cells. Another type, like sweat glands for example, is *merocrine* in character, that is, the glands continue to elaborate secretions without fatal results to their structural units.

The simple one-celled glands of lower forms, such as the mucous glands in the hypodermis of an earthworm, have at first a surface exposure to the outside world. As glandular needs increase with the enlargement of the body, and the amount of available outside surface becomes inadequate, they push down into the underlying corium, thus adding enormously to the total secreting area without taking up any more room at the surface, just as large bays and inlets increase greatly the actual extent of the coast line between two points as a crow flies.

Many-celled epidermal glands which occur in land forms higher up in the scale are either *tubular* or *alveolar* (Fig. 151), and may be either simple, branched, or compound. The amount of space that a compound gland occupies at the surface is relatively small, being represented simply by a tiny pore for the escape of the secretion produced.

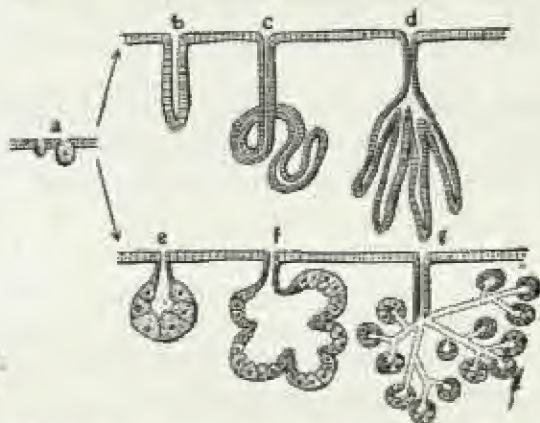


Fig. 151. Diagrams of various types of glands, shown as invaginations from a layer of indifferent epithelium. A, primitive unicellular glands; a, simple tubular gland; c, coiled tubular gland; d, branched tubular gland; e, simple alveolar gland; f, compound alveolar gland, with a single duct; g, more highly differentiated alveolar glands, with compound ducts. (Modified from Wilder.)

(b) **Invertebrate Skin Glands.**—Representatives from nearly every phylum of invertebrates exhibit integumentary glands of various sorts that serve a variety of purposes. The Cnidaria among coelenterates receive their name from the wide-spread occurrence of glandular stinging cells, or *nematocysts*, in the ectoderm, by means of which small prey is paralyzed, and the attacks of enemies probably are warded off.

Sedentary animals in some instances may gain anchorage by glandular activity. Thus, the *cement glands* of barnacles enable these curious crustacean cousins of the crabs to stand on their heads, securely fastened within their protective shells, in which position they can tranquilly kick food into their mouths in safety.

Many mollusks also, for example mussels, attach themselves to some solid foundation by the secretion of tough byssal threads from a *byssal gland*. Even microscopic rotifers, as they inch along, manipulate their tiny bodies by the aid of a sticky *tail gland*, while the lacquered cocoon in which an earthworm deposits its underground eggs is secreted by the glandular *clitellum*.

Many insects produce glandular secretions. The defensive odor of "stink bugs," the protective millinery of woolly aphids, the poisoning or irritating power of myriapods, spiders, and brown-tail moths, as well as the thread and web spinning of caterpillars, are all due to the activity of hypodermal glands. Anyone who has picked up a fat-bodied blister beetle (*Meloë*) will remember the acrid yellow "elbow grease" that exudes glandular unfriendliness from its joints. Bee's wax is another product of invertebrate integumentary glands.

(c) **Vertebrate Glands.**—The almost universal epidermal glands of fishes are superficial one-celled *mucous glands*, which are widespread both over the surface of scales, and wherever naked skin occurs. They are supplemented by two kinds of less common glandular cells, namely, *granular gland cells*, which are especially abundant throughout the epidermis of cyclostomes (Fig. 144), and more deeply lying *beaker cells* that frequently extend from the Malpighian layer all the way to the surface. All three of these kinds of glands contribute to render fishes slippery and hard to grasp. Doubtless too by lubrication they may facilitate to a certain extent the passage of these submarines through the water, also effecting the constant removal of foreign substances that may adhere to their bodies.

The African lungfish, *Protopterus*, has skin glands that secrete a varnish-like cocoon in which the animal aestivates, buried in the mud, thus surviving the dry season.

Pterygopodial glands, associated with the pelvic "claspers" of male dogfish and other selachians, are multicellular mucous glands having to do with copulation.

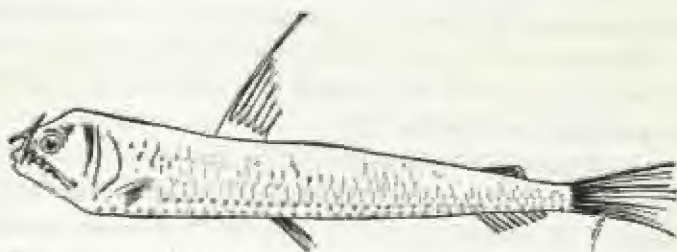


Fig. 152. A deep-sea teleost, *Chauliodus*, with a double row of luminous organs on either side of the body. (After Lendenfeld.)

Deep-sea fishes, that live in a world of darkness where no ray of sunlight can penetrate, are in many instances equipped with glandular integumentary organs of considerable complexity, which produce light. These *luminescent organs* (Fig. 152) are practically the only many-celled glands in the skin of fishes. They are usually accompanied in those species possess-

ing them by enormously large eyes adapted for catching the faintest glimmer of luminescence, so that when Diogenes of the Deep Sea fares forth, his lantern may not pass by unnoticed. Other deep-sea fishes, without light-producing organs, are usually entirely blind or have only very degenerate eyes.

Certain fishes, as well as amphibians and reptiles, also have integumentary cells of a glandular nature, called *chromatophores*, by means of which the color of the body may be modified to conform to the color of the environment in which the animal temporarily finds itself. It has been demonstrated by Parker that the operation of these color changes depends not so much on direct stimulation through the nervous system as upon certain "neurohumors" or hormones produced by ductless glands within the body.

With the exception of the so-called *Leydig's glands* found in the larvae of some anurans, one-celled epidermal glands, so characteristic of the fish skin, do not appear in *amphibians*, being replaced by many-celled alveolar glands which also provide mucus.

One of the functions of the skin glands of both fishes and amphibians, that does not recur as an integumental activity in higher vertebrates, is the production of irritating or poisonous substances as a means of defense against enemies. In fishes such *poison glands* are usually at the base of puncturing spines or sharp fin rays, but in amphibians they are more generally distributed over the body. Toads, for example, are usually left alone on account of the noxious secretions from their skin glands. The glandular rings that alternate with the tiny embedded scales of the blind caecilians are equipped not only with many-celled mucons glands, characteristic of amphibians, but also with peculiar *giant poison glands* (Fig. 148).

Another function of epidermal glands is shown by tree frogs (Fig. 153) and certain salamanders which have *glandular feet* that enable them to stick to vertical surfaces, and by some male frogs that are unique in having glandular thumbs swollen during the breeding season, making it possible for them to saddle on to the slippery backs of the females until the extrusion of the sperm and eggs is accomplished (Fig. 154).



Fig. 153. Tree frog, showing glandular sucking discs at the ends of the toes. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers.)

Epidermal glands are much reduced in *reptiles* and *birds*, and whenever they do appear are quite localized. For instance, from neck to tail



Fig. 154. Right fore foot of a male *Frog*, *Rana esculenta*, showing the epidermal swelling on the radial side, which appears temporarily during the breeding season, and is an aid in grasping the female securely during amplexation. (After Leydig.)

down the long back of an alligator there is a crowded row of degenerate glands between the first and second row of scales on either side of the midline, the use of which has not been determined. On the underside of the lower jaw also there is a pair of evertible glandular structures that during the mating season give forth a strong musky odor which probably has something to do with the sexual psychology of these animals.

Similar *odoriferous glands* occur in other reptiles. They are a most notable possession, for example, of the "stink-pot" turtle, whose scientific name, *Aromochelys odorata*, is almost as descriptive as its common name. Odor glands are located particularly about the cloacal opening of copperheads and certain other snakes.

The so-called *femoral "glands"* of male lizards, extending in a row along the inside of each hind leg from knee to cloaca like a row of tiny portholes (Fig. 155), produce a dry gummy secretion which hardens into short spines, or "teeth" (Fig. 156), that are useful as a holdfast gripping device during copulation.

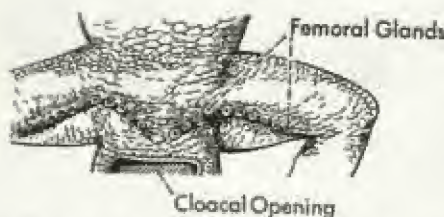


Fig. 155. Femoral "glands" of male *Lacerta*, probably useful in grasping the female during copulation. (After Maurer.)

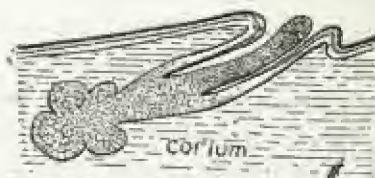


Fig. 156. Section through a single femoral pore (Fig. 155) of a lizard, *Lacerta*, showing projecting plug of dry cells that may help to prevent slipping during copulation. (After Bütschli.)

The *uropygial*, or *preening glands*, are best developed in water birds, and are reported as being odoriferous during sexual activity, which suggests that their ancestral function was sexual allurements, although their chief use now has come to be that of supplying pomatum for use in preening. They are paired structures usually with a single outlet from which the bird

squeezes out the greasy secretion with its beak when dressing the feathers. In ducks and pelicans there are several ducts, instead of a single opening, that allow the oily secretion to escape.

Aside from this curious uropygial gland at the base of the tail, the only other integumental glands found in birds are oil-glands in the external ear passages of certain gallinaceous birds, like the European capercaillie (*Tetrao urogallus*), and the American turkey.

Integumental glands reach their greatest variety and differentiation in the mammalian skin. Never unicellular, they are either tubular or alveolar in character.

(d) **Sweat Glands.**—*Sweat glands* are the most common and generally distributed of mammalian tubular glands. Dr. Oliver Wendell Holmes, in his delightful lectures to Harvard medical students, likened sweat glands to "fairies' intestines." Each one is an elongated tube, the walls of which are composed of cells (Fig. 157). The deeper glandular portion is usually coiled up to occupy a minimum of space, while the outermost part, that serves as a duct and opens at the surface with a funnel-shaped pore, often spirals like a corkscrew as if it found difficulty in penetrating the compacted outer corneal layer of the skin. Although originating in the epidermis like all other integumentary glands of vertebrates, sweat glands by a process of growth push deep down into the corium where their terminal coiled parts come into intimate contact with the capillaries, making possible the extraction of sweat from the blood.

In a healthy man the fluid sweat, visible and invisible, amounts to a daily loss of from one to five pints, and in extreme instances to as much as two per cent of the entire body weight. It has been estimated that there are two and one half million sweat tubules in an average human skin each with a separate pore just at the limit of visibility to the naked eye. Stated more graphically, there are about four hundred printed words on this page, and in the entire book approximately one eighth as many words as sweat glands in the author's skin, all of which it might be added have been exercised in laboriously arranging the letters as they stand.

Sweat glands in the human skin are not equally distributed, being more numerous on the palms and soles than elsewhere, and attaining a notably greater size under the arm pits.

Racial differences in the abundance of sweat glands have been observed, as shown in the following counts per square centimeter on the finger tips:



Fig. 157. A sweat gland. A, a network of capillaries inside of which lies the coiled end of a sweat gland, B. [After K mber.]

American, 558; Filipino, 653; Negrito, 709; Hindu, 738.* Negroes can endure the tropics better than the whites because they are more generously supplied with sweat glands. There is so much individual variation in whites with respect to the ability and ease to perspire, that army authorities of England and the Netherlands take cognizance of this fact and do not detail for service in their tropical colonies those men who are unable to sweat freely.

In mammals that are abundantly clothed with hair, the sweat glands become crowded out or localized in restricted areas. Thus, in cats, rats, and mice these glands are confined to the soles of the feet; in bats, to the sides of the head; in rabbits, to an area around the lips; in deer, to the region at the base of the tail; in shrews, to a line down either side of the body; in ruminants, to the muzzle and the skin between the toes; while in the hippopotamus sweat glands occur only on the ears, which are the parts of the body of these semi-aquatic monsters most exposed to air. Sweat glands are wanting in *Echidna*, some insectivores and the water-dwelling sirenians and cetacea.

The male of the giant kangaroo is named *Macropus rufus* because its sweat is reddish in color, and the African antelope, *Cephalophus pygmaeus*, is said to produce albuminous sweat that forms a bluish lather. It will be remembered that in the "horse and buggy days," when a harness chafed an overheated horse, white lather appeared because of albumin present in the sweat.

The *ciliary* (*cilium*, eyelash) *glands of Moll*, that are the center of trouble whenever a sty is formed, are modified sweat glands.

(c) **Sebaceous Glands.**—While tubular glands are confined to mammals, alveolar glands of various kinds occur not only in the mammalian skin but also in the skin of other land vertebrates as has already been noted.

The most universally distributed of the mammalian alveolar glands are *sebaceous glands* which produce an oily secretion (*sebum*), usually in connection with hairs (Fig. 158), although they are also found independent of hairs at the edge of the lips and about the genitalia, where the skin passes over into the mucous membrane. On the tip of the nose, particularly the bulbous noses of the indulgent, middle-aged type, the openings of the free sebaceous glands may be seen as tiny pits, marking the locality of ancestral hairs that have been lost in the evolutionary shuffle.

Sebaceous hair-follicle glands number frequently two or three to each hair, opening into the pocket from which the hair shaft projects, rather than directly upon the surface. The size of sebaceous glands is not in relative

* *Anat. Rec.*, 1917, 1.

proportion to the size of the hairs with which they are associated. They frequently become enlarged in the absence of hairs, which suggests that their primary function is not so much concerned with oiling the dry hair, as is commonly assumed, as with providing the surface of the skin with a filmy coating of oil.

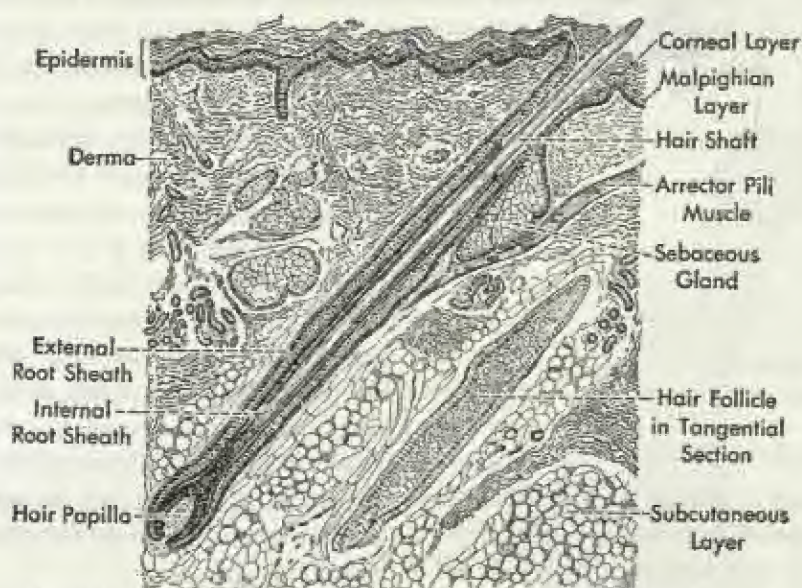


Fig. 158. Relation of the various parts of a hair and its follicle to the parts of the integument.

The two-toed sloth, *Choloepus*; the Cape mole of South Africa, *Chrysochloris*; the scaly anteater, or "pangolin," *Manis*; and the water-inhabiting sirenians and cetaceans, already cited for their lack of sweat glands, are equally deficient in sebaceous glands, although the first two are abundantly hairy animals.

(f) **Other Alveolar Integumentary Glands.**—Along the edge of each eyelid there is a line of modified sebaceous glands, called *tarsal* or *Meibomian glands* (Fig. 717), which produce an oily film across the exposed part of the eyeball between the edges of the eyelids and the eyeball itself, a film that retreats and advances with every wink. This oil seal ordinarily retains a film of tears which constantly moistens the surface of the eyeball. In the case of weeping the oily dam is broken by the flood pressing from behind, and tears trickle down the cheeks (Fig. 159).

Another kind of integumentary alveolar glands is associated with sexual activity in various mammals. These structures should not be confused in any

way with the so-called primary "sex glands" which produce eggs and sperm, since they are derivatives of the epidermis having usually only a lubricating function in connection with the genital organs. Examples of such glands



Fig. 159. Diagram of the evolution of the lacrimal glands. a, position in amphibians; b, in reptiles and birds; c, in man. Sometimes in man the lacrimal glands are found located in the "b" position. (After Wiedersheim.)

are the *preputial* and *vulval glands* in the male and female respectively, and *scent glands* which act as an allurement to the opposite sex. These latter glands are usually located near the anus, as in the musk deer, beaver, civet cat, dog, fox, and skunk. The scent glands between the toes of goats, whatever their effect on humankind, may have a meaning for the goats themselves.

In the external ear passages of most vertebrates are found the *ceruminous* or *wax glands*, which in form show affinities with the tubular type but in function resemble sebaceous glands, since they produce a gummy or waxy secretion more like oil than sweat. They serve to arrest dust particles, and to discourage adventurous crawling insects that might otherwise be tempted to invade the sacred precincts of the ear, a function not so apparently needful in the case of man as of a dog sleeping in the sunshine with a halo of busy insects buzzing around its head.

(g) **Mammary Organs.**—Of paramount importance in the life of mammals are the *milk glands* which characterize this order of vertebrates. The mammary glands, although resembling the necrobiotic sebaceous glands in structure, are intermediate in method of secretion between sweat and sebaceous glands. Their derivation in all probability should be traced not to sweat or sebaceous glands, but to some common ancestral type less differentiated than either. Their activity is periodic instead of continuous and, for the most part, finds expression only in the female.

The mammary apparatus includes not only the *mammary glands* themselves, but also the elevated *nipples*, that furnish an outlet for the glands, and *breasts*, or *mammæ*, which are integumentary swellings produced by the localized presence of the enlarged mammary glands in the skin (Fig. 160).

The normal number of *nipples* varies from two in the horse, bat, whale, elephant, and man, to twenty-five in the opossum, *Didelphys henseli* (Fig. 161). Carnivores usually have six or eight; rodents, two to ten; pigs, eight to ten; and ruminants, four. In those species where several young are born in a litter there is a corresponding provision in the number of nipples.

The number of ducts per nipple that drain the glands is also subject to considerable variation. In mice, ruminants, and insectivores, there is only one; in the pig, two or three; and in carnivores, three to six. In man there is a cluster of about twenty separate ducts opening into each nipple.

Milk, which is secreted by these glands, is the natural food of young mammals. It is composed of water derived from the blood stream, butterfat, milk-sugar, albumin, and certain salts in varying proportions. Albumin in milk favors rapid growth of the young. The milk of a reindeer, which lives in a habitat where it is desirable for the young to attain enough maturity to care for themselves as soon as possible, has a large albumin content. The guinea pig, whose milk contains approximately ten per cent of albumin, doubles its weight after birth in six days, while the human infant feeding upon milk with less than two per cent of albumin, requires 180 to 200 days in which to double its weight. Other factors, in addition to the kind of milk, enter into this difference in rapidity of growth, but the fact is apparent that different kinds of milk are adapted in nature to different requirements.

Mammary glands may develop in various places on the mammalian skin. Instances are recorded in medical literature of the abnormal occurrence in human beings of mammae under the arm pits, on the shoulders, and even upon the hips. Their normal distribution in different species of mammals, however, holds a definite relation to the accessibility of the nipples to the suckling young. Thus in carnivores and swine, which attend to their nurslings while lying flat on the side, the nipples are arranged in two rows along the ventral side of the body. Those quadrupeds which habitually stand while nursing their young usually have the nipples in a protected situation between the legs, either anterior as in elephants, or posterior as in cattle and horses, while the nurslings brace themselves on stiltlike legs as they drain the maternal udders. Arboreal animals that hold their "babes in

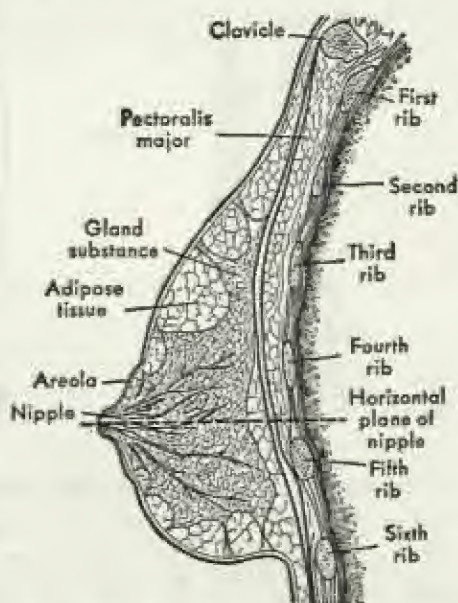


Fig. 160. Diagram of a human mammary gland. (From Woodruff, *Animal Biology*, copyright 1941, by permission of The Macmillan Company, publishers. After Gerrish.)

arms" have conveniently located pectoral nipples. Mankind, with a probable arboreal ancestry, also has pectoral nipples. The grotesque sea-cows, which enfold their single offspring between their anterior flippers and "stand" with the head elevated out of the water, likewise have pectoral nipples. This circumstance has no doubt contributed to the mermaid myths among sailors who have chanced to glimpse at a distance the intimate family life of these rare strange creatures.



Fig. 161. Arrangement of nipples in *Didelphys henryi*. (After O. Thomas.)



Fig. 162. The flying lemur, *Galeopithecus*, "whose offspring literally cling for dear life to the breasts of their floppy mothers." (After Hiltzheimer.)

Unlike the young of the sea-cow, the baby whale (Fig. 74) is a marine "trailer," for the maternal nipples from which it secures milk while navigating the high seas are situated far posterior on either side of the sexual orifice entirely out of the mother's sight, in pockets which fit over the snout of the baby whale in such a way as to minimize the chance of the milk becoming too much diluted with salt water.

The opposite extreme to the position of nipples in the cetaceans is found in the topsy-turvy bats and flying lemurs (Fig. 162), whose offspring literally "cling for dear life" to the breasts of their aerial mothers, the accessible nipples of which are axillary in location, or under the arm pits.

The development of the mammary apparatus is initiated by the formation of an epidermal ridge down either side of the belly from axilla to groin, called the *milk-line stage* (Fig. 163). It appears in man near the beginning

of the second fetal month when the embryo is still less than half an inch in length. The milk-line stage is succeeded by the *milk-hill stage* (Fig. 163), which results when the epidermal ridge of the milk-line becomes absorbed except for a beadlike row of remnants, each one of which marks the possible location of a future mammary gland. These tiny milk-hills are compact masses of cells that later sink down into the underlying tissue, leaving no



Fig. 163. Early stages in the development of the mammary apparatus. A, milk-line stage in a pig embryo of 1.5 cm; B, milk-hill stage in a pig embryo of 1.9 cm. (After O. Schultze.)

visible trace of the developing mammary apparatus. The double row of depressed "hills," thus embedded in the corium, becomes the *milk-field stage*. As the leveled hills of the milk-field stage sink deeper and become valleys, there is formed where the hills formerly were a double row of pits along the lateral walls of the belly, converging posteriorly from the anterior region. This represents the *milk-pocket stage* (Fig. 164c). It is the cells that line the sides and bottom of these milk pockets which directly give rise to the mammary glands.

In forms that do not have two complete rows of nipples, some of the pockets fail to develop. In man, for example, it is the fourth pair of embryonic milk pockets at the anterior end that become the permanent mammae.

The final differentiation of the mammary apparatus takes place when the milk-pocket stage is succeeded by the *nipple stage*. According to the two ways of their formation *true* and *false* nipples are distinguished. Among marsupials, rodents, and primates the floor of the milk pocket, into which the ducts of the mammary glands open, elevates, carrying the elongated ducts of the milk glands with it, thus causing them to open at the tips of the *true nipples*. In the case of *false nipples*, which characterize pigs, carnivores, horses, and ruminants, the floor of the milk pocket with its ducts remains unelevated, while the margins of the pocket pull up all around to form a

hollow nipple. There is thus formed a secondary tube or elongation upward of the milk pocket itself, called the *milk canal*, into which the mammary glands pour their secretion, to be pumped to the tip of the false nipple.

The mammary apparatus develops equally in both sexes up to the time of puberty, when it degenerates in the male and becomes potentially functional in the female. The male may produce milk, as in the primitive monotreme *Echidna*, and also in exceptional instances among higher mammals, even in man. Such abnormal behavior is termed *gynecomastism*.

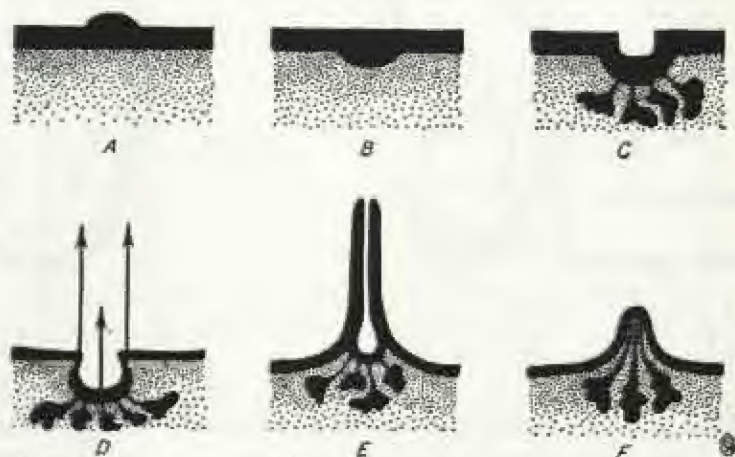


Fig. 164. Development of the mammary glands. A, diagrammatic cross section through the milk-line (Fig. 163A); B, the epidermal milk-line, after breaking up into a chain of isolated milk-hills (Fig. 163B) has sunk down into the corium (dotted) and is no longer apparent externally, thus forming the milk-field stage; the levelled area, where the milk-hills were, becomes depressed, C, forming the milk-pocket stage. The sunken epidermal plug penetrates still deeper into the corium, giving rise to the mammary glands, D, preliminary indifferent milk-pocket stage, with the two longer arrows indicating the direction of epidermal growth that results in the formation of a "false nipple," while the short arrow shows how the "true nipple" forms; E, false nipple, with ducts of the mammary gland opening at the bottom of a milk-canal; F, true nipple, with the mammary ducts opening directly at the tip.

In man as well as other mammals, extra nipples (*hyperthelism*) (Fig. 165) not infrequently occur, as also do extra breasts (*hypermastism*) (Fig. 166). Such persistent embryonic relics, particularly in the case of hyperthelism, occur quite as often in males as in females. Usually these supernumerary parts are arranged along the vanished embryonic milk-line.

The mammary apparatus of monotremes presents many exceptions to that of other mammals. Instead of being alveolar in form the mammary

glands are branched-tubular, producing a sort of nutritious sweat instead of the usual milk (Fig. 167). No nipples are present, tufts of hair serving in their stead. The young monotreme does not have muscular lips and is further handicapped by a horny beak. In consequence it is quite unable to suckle, so it licks the nutritious sweat from the makeshift tufts of hair on the mother's breast, with its protrusible tongue. The skin on the belly of *Echidna* forms a temporary pouch, or *incubatorium*, that surrounds the mammary area while the young are being cared for. Into this pouch is deposited the single leathery-shelled egg, which soon hatches into a very premature helpless embryo, there to undergo the preliminary perils of early development which other mammals accomplish in greater safety within the protective uterus of the mother.



Fig. 165. Hyperthelism. Three supernumerary nipples are shown. (After Martin and Mollison.)

Even an incubatorium is lacking in *Ornithorhynchus*, which broods its egg in a hole in the ground that serves as a nest. The ventral mammary area is depressed, as in the milk-pocket stage of development, and from the depression tufts of hair project, which serve as nipples. It is probable that gynecomastism occurs in both *Echidna* and *Ornithorhynchus* with both parents sharing in the feeding of the young.

Most marsupials regularly possess a permanent pouch for carrying the immature young (Fig. 55c), although between incubations it may decrease somewhat in size. In the Didelphyidae to which the opossum belongs, the

marsupium, or pouch, is mostly wanting or represented by two insignificant folds of skin. True nipples are present within the marsupium and typical milk glands supply real milk. The nipples project, however, only during lactation. At other times, like a disappearing gun, they retract within a surrounding pit in the skin. The young marsupial retains its hold on the nipple within the enveloping edge of the marsupium by

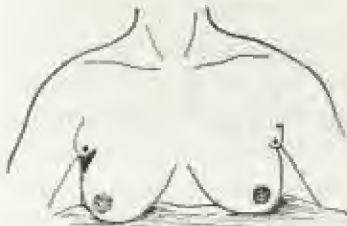


Fig. 166. A case of hypermastism. (After Hansemann.)

means of powerful muscles around its mouth (Fig. 54). At first the young animal is so helpless that it can only stay passively attached to the nipple, and it is necessary for the mother to pump the milk down its waiting throat

by means of the contraction of breast muscles. Later, as it becomes able to use its own muscles and nerves, it feeds itself as ordinary mammalian youngsters do, by its own efforts.

Young marsupials, even after they attain considerable size and have gained some degree of independence, are glad to retreat into the maternal marsupium on the approach of danger.



Fig. 167. Ventral view of *Echidna* with the skin loosened on one side to show the mammary glands. (After Semon.)

In placental mammals the marsupial pouch disappears, since the fetus is cradled in greater safety within the uterus until at birth a stage of development has been reached that makes bodily protection on the part of the mother less imperative. There are, however, certain dim vanishing reminders of a marsupial pocket around the nipple even in the human embryo, for at about the beginning of the second fetal month, when the future mammary apparatus is being set up, there develop around the milk-hills transitory epithelial thickenings that possibly represent the last remnants of an ancestral marsupium (Fig. 168).

The long period of obligatory milk-feeding among the higher mammals not only allows ample time for more extended development of the young but is also a necessary preliminary to the invaluable *process of learning* through prolonged association with the parent. This opportunity is denied to all those unmothered kinds of animals that are born equipped with instincts which make it unnecessary for them to learn how to live. The dominant mammals are fortu-



Fig. 168. Reconstruction of transitory epithelial structures around the mammary glands in the skin of a human fetus 56 days old. The dotted circles represent the area where the budding arms joined the body. The two large black dots are the epidermal "milk-hills" that are to give rise to the mammary glands, and which locate the position of the future nipples. The twenty-one smaller black dots are epithelial thickenings around the nipples, which may be the vanishing remains of ancestral marsupial pockets. (After Walter, in *Anat. Anz.* XXII, 1902.)

nate because they must work out their salvation by *learning how*, and have been endowed with the capacity to do it.

2. Scales

(a) **Fishes.** While every class of vertebrates except cyclostomes has some representatives with a scaly skin, the presence of scales may be regarded as the most notable modification of the integument of fishes and reptiles. Whenever fishes lack scales, as for example many Siluridae and certain bottom-feeding forms, it is to be regarded as a secondary modification and not the primary ancestral condition. Even in the case of the apparently naked eels, tiny vanishing scales appear for a time in the embryonic stages.

There are at least four general kinds of *fish scales* of particular interest to the comparative anatomist, namely, *placoid*, *ganoid*, *cycloid*, and *ctenoid*, not including bony dermal plates that reached a high degree of elaboration in extinct ostracoderms (Fig. 17), and other armored fishes of early geologic times.

The most primitive fish scales are *placoid*, appearing first in the ancestral sharks of the Upper Devonian times, and found today among selachians generally. In structure a placoid scale consists of a somewhat flat, basal plate originating from the corium and embedded in it, and usually carrying a spiny projection of toothlike dentine capped with a harder substance considered by some observers to be enamel, formed by epidermal cells, but regarded by others as a special type of dentine, produced by dermal cells.

The obvious transition in both structure and position from placoid scales of the skin on the outside of the head, to the rows of teeth within the inner margin of the shark's jaws is so continuous and unmistakable that tooth may be regarded as modified placoid scales (Fig. 169). The basal dermal plate of the scale corresponds to the root of a tooth, while the projection of dentine and its enamel cap are quite like similar familiar parts of a typical tooth (Fig. 240). These relationships are not surprising to one who remembers that the lining of the anterior part of the digestive tract, formed from a stomodaeal invagination, is really modified epidermis.

Placoid scales in dogfishes and sharks are usually small and closely set without actually overlapping, although their backward-projecting enameled

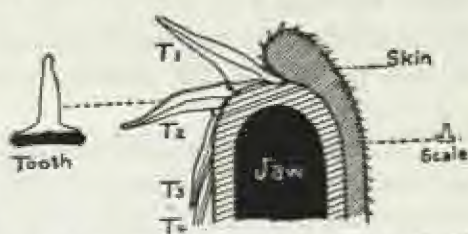


Fig. 169. Diagram of the edge of a shark's jaw, to show the relation of placoid scales and teeth. T_1 , tooth in service at the edge of the jaw; T_2 , T_3 , T_4 , reserve teeth.

spines aid in effecting protection of the spaces of skin between the embedded scales. Pavement scales of various shapes may give added protection to the most exposed areas. Before the invention of sandpaper and emery cloth, the rasping "shagreen" skin of dogfishes and sharks, which is covered with sharp, thick-set placoid scales, was frequently used by cabinet makers for putting the final smooth finish on wooden surfaces. Quite large placoid scales equipped with jagged spines appear in skates and rays and are often localized in certain exposed areas, as down the median line of the back, leaving scaleless patches of skin unprotected.

Ganoid scales of considerable diversity are the common characteristic feature that stamps the ganoid fishes. The few genera of ganoids living in fresh waters today are the last survivors of a large populous and diversified order of fishes which once ruled the Devonian seas. Their scales furnish a



Fig. 170. Ganoid scales of *Lepidosteus*. Three of them are perforated by openings of the lateral line organs.

variety of form and structure out of all proportion to the number of species involved. In the sturgeon, *Acipenser*, for example, they are large isolated bony scutes, not entirely covering the skin but located in exposed situations on the body where there is the greatest wear and tear, like the rows of brass-headed nails decorating the edges of great-grandfather's chest.

In the garpike, *Lepidosteus* (Fig. 170), on the other hand, as well as in the related forms *Calamoichthys* and *Polypterus*, the scales are hard polished rhombic plates fitting edge to edge, or very slightly imbricated one over the other, thus forming a complete armor. The skin of the spoonbill sturgeon *Polyodon* is almost entirely without scales, while in *Amia* modified ganoid scales occur on the head but only cycloids in the trunk and tail regions.

The scales of fossil ganoids are quite large and platelike, just as in living survivors of the group where scales that cover the head sometimes become enlarged into dermal scutes which take part in the formation of the investing skull bones.

The outer surface of scales of this type is composed of *ganoin*, a hard shiny substance secreted by the corium, not at all homologous with the ectodermal enamel that caps placoid scales. This material is not present, however, on the ganoid scales of *Acipenser*, *Scaphirhynchus*, and *Amia*. The main underlying part of ganoid scales is made up of *isopedin*, a connective tissue substance in which bone cells are embedded and which like bone is penetrated by Haversian canals containing capillaries.

Louis Agassiz distinguished two kinds of scales in teleosts, which he named cycloid and ctenoid. *Cycloid scales*, as the name indicates, are rounded in shape (Fig. 171) and thicker in the center, thinning out towards the margin. They overlap like shingles and if spread over a surface like ganoid scales edge to edge would much more than cover the body. They are, however, embedded in pockets of the corium with only a part of the outer smooth margin exposed. Since they project diagonally at an acute angle with the surface of the skin, and overlap their neighbors, the entire body is protected by at least a double thickness of scaly armor at every point. Present-day bony dipnoans as well as *Amia* and some teleosts have cycloid scales.



Fig. 171. Cycloid scale of a salmon showing lines of growth. (After Hesse.)

Ctenoid ("comblike") scales, also rounded in form, have in addition projecting teeth on the surface of the exposed areas (Fig. 172). All intermediate types between the cycloid and the ctenoid stages are to be found.

In some fishes, as for example certain flounders, the scales on the upper side are ctenoid, while those on the under side are cycloid. Of these two types the cycloid scale is the more primitive, occurring first in the fishes of the Jurassic Period, while the ctenoid type did not appear until Cretaceous times.



Fig. 172. Ctenoid scale. (After O. Hertwig.)

Both cycloid and ctenoid scales are entirely dermal in their origin. The *scleroblasts*, or scale-forming cells in the corium, lay down two layers of different substance in the formation of a scale. The outer layer is homogeneous and bony, while the under side is fibrillar and contains calcareous deposits. Such scales increase in thickness and area by the activity of the *scleroblasts*, successive additions being indicated by concentric lines of growth like similar rings of growth exhibited in the cross section of a tree trunk. Inasmuch as periods of growth alternate with comparative inactivity in the case of most fishes, according to the seasonal variation of their food supply, it is possible to estimate the age of a fish by an examination of the diary-like lines on its scales.

In addition to marginal lines of growth, certain radial grooves are also present, caused by the failure of the outer homogeneous layer of the scale to be deposited in these places. Such radial grooves add somewhat to the flexibility of the individual scale, a very desirable feature since teleost scales, although thinner than the edge-to-edge ganoid type, by reason of their

shingling arrangement, form a double envelope over the underlying muscles that might hamper free movement.

Some teleost fishes, for example, the pipefish *Syngnathus*, and its curious relative, the seahorse *Hippocampus*, do not have overlapping scales but instead are encased in a cuirass of bony plates.

(b) **Amphibians.** Scales in all modern amphibians are absent, except for the tiny bands of scutes embedded in the skin of the tropical legless caecilians (Fig. 148).

The extinct stegocephalans that flourished in Devonian times were characterized by bony plates in the skin, particularly on the ventral side of the body.

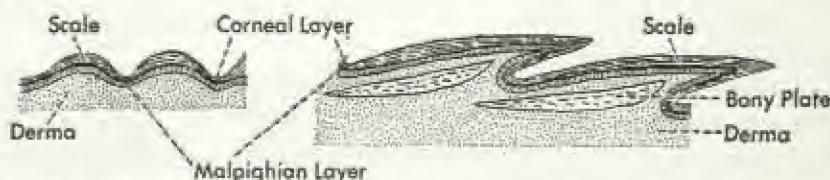


Fig. 173. Diagrammatic longitudinal sections through reptilian integument. Scales occur as localized thickenings of the corneal layer of the epidermis. (After Boas.)

(c) **Reptiles.** Reptiles are represented today by only a few divergent specialized types, namely, lizards, snakes, turtles, crocodiles, alligators, and *Sphenodon*. Superficially quite unlike each other these survivors agree, so far as scales are concerned, in the predominant part that the epidermis plays in their formation. Small dermal plates, or *ossicles*, sunken in the corium and spaced with much regularity, are present in most reptilian species, although many lizards and snakes lack them. When present they are covered over by a continuous layer of epidermis in which the dry outer corneal part becomes thickened or embossed wherever it covers an ossicle. It is thinner and more flexible between the thickened parts or scales of the epidermis, thus allowing some freedom of movement (Fig. 173). Even in a skin without ossicles the corneum thickens into epidermal scales that hang together in a continuous sheet. Thus they form an unbroken armor in which the scales cannot be scraped loose, as may the separate independent dermal scales of teleost fishes.

As already mentioned the entire dry corneal part of the skin of snakes periodically loosens and is cast off. Such is not the procedure with turtles and alligators, for in these animals the corneal scales that overspread the dermal plates in the skin are discontinuous and the demands of increasing size are met by concentric marginal increments of growth which are added

to each scale. The highest development of this underpinning of ossicles is reached in the armored turtles, although some of the extinct dinosaurs were "fearfully and wonderfully made" with respect to dermal scales.

Many reptiles, like the "horned toad" *Phrynosoma*, and *Sphenodon* and the alligators and crocodiles, exhibit spines or embossed patterns on the epidermal scales, while the head of a snake, which has to poke about between obstacles, is entirely ensheathed by large platelike scales, with the sense of touch that is thereby excluded from the surface of the head transferred to the delicate protrusible tongue.

(d) **Birds.** There is very little to say about scales in the skin of birds, since aviation has no use for such heavy clumsy structures. Only on unfeathered areas, such as the shanks and around the base of the beak, is the epidermis thickened and cornified into a semblance of reptilian scales, and nowhere do dermal ossicles occur under corneal thickenings.

(e) **Mammals.** Scales, although generally replaced by hairs in mammals, still persist in a number of instances. Mammalian scales are epidermal like those of reptiles.

They are large horny and imbricated in the scaly anteater, *Manis* (Fig. 65A), although absent on the ventral side of the body. During ecdysis they are shed and renewed singly. In armadillos no ecdysis occurs but growth is accommodated within the shieldlike armor by marginal accretion of the separate scales as in turtles. Areas of bare skin between the rows of scales permit these animals to roll up into a ball for the purpose of defence. Their fossil forbears, the giant glyptodons of South America, could not roll up, but their thick fused scales made such an impenetrable barrier, like that of a war tank, that they must have been practically carnivore-proof. The fact that telltale hairs project between the scales of armadillos proclaims them to be mammals, although bearing a "wolf's clothing" of scales.

A great variety of mammals have scaly tails reminiscent of earlier forebears, the beaver, rat, mouse, opossum, mole, shrew, and certain lemurs. Scales even appear on the back of the paws of moles and shrews, and it will be remembered that the fetuses of the brown bear and European hedgehog (Fig. 150) testify to some sort of a scaly pattern in the past by developing transient useless embryonic scales over the back. Only the armadillos have bony plates beneath their scales.

3. Horns

The earliest known horns appear as bony projections on the heads of certain ceratopsid dinosaurs whose skeletons have been recovered from the Cretaceous beds of North America. For instance, *Triceratops*, as its name

indicates, sported a horn over each eye and a third one on its nose (Fig. 36F and H). Even among modern reptiles there are a few rare bizarre lizards with nose horns, for example *Chamaeleon oweni* and *Ceratophora stoddarti* (Fig. 174). The "horned toad," *Phrynosoma*, of our southwestern desert region, also a lizard and not an amphibian as its name would imply, is another reptilian specialist in horns (Fig. 43). Aside from these few cases of horned lizards, horns are peculiar to mammals and are coupled with hoofs that characterize the ungulates.



Fig. 174. Head of a male lizard, *Ceratophora stoddarti*, with a horn on its snout. (After Darwin.)

In early Triassic times certain ungulates that lived in North America outdistanced dinosaurs in the number of their horns. *Dinoceras*, for example, had six large horns on its head. It is probable that these conspicuous bony projections were capped over by horny sheaths, although positive evidence is not furnished by the fossils of these animals.

There are four general kinds of ungulate horns known today, namely, keratin-fiber horns, antlers, pronghorns, and hollow horns.

(a) **Keratin-Fiber Horns.** Keratin-fiber horns are made up of hairlike keratin fibers produced from the corneal layer of the epidermis and cemented together in a hard compact mass. They are entirely epidermal and have no bony core. The Indian rhinoceros carries one of these horns on its "nose," as its name indicates (*rhino*, nose; *ceros*, horn), while the African rhinoceros has two, arranged tandem-fashion instead of side by side in the conventional way of paired structures (Fig. 66c and d). It is reported that *Bos triceros*, one of the kinds of native African cattle, also has a median horn of this curious type, as its species name indicates.

(b) **Antlers.** Antlers are commonly borne by the various representatives of the prolific and diversified deer family (Cervidae), ordinarily only by the



Fig. 175. The growth of antlers. a, April 2; b, April 20. (After Stone and Gram.)

males, but in the case of the reindeer and the caribou by both sexes. They consist of bony outgrowths from the skull, which at first are entirely covered over by hairy skin. While in that condition a stag is said to be "in velvet" (Fig. 175). Later the skin dries and becomes rubbed off, leaving the antlers as unadorned bone, at which time it is incorrect to include them among

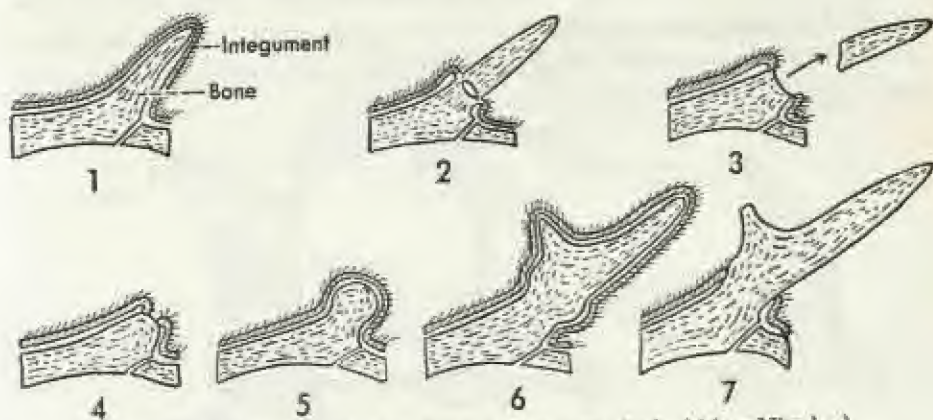


Fig. 176. Diagrams showing how antlers are shed. (After Nitsche.)

integumental structures. At the end of the second year, before the mating season, the antlers weaken at the base next to the skull by the breaking down and absorption of some of the bony tissue, and are broken off. The surrounding skin grows over the wound thus made and a new pair of antlers "in velvet" grows out (Fig. 176); this time with an additional prong. Thereafter each successive breeding season is celebrated by new antlers, usually with a regular increase in the number of prongs (Fig. 177). This physiologically expensive process of shedding and renewing the antlers does not occur in castrated bucks, which is evidence that it is determined by the secretion of sex hormones. The antlers of the fossil Irish elk that once roamed the boglands of Ireland grew to an enormous expanse, as if they started and could not stop. Doubtless their excessive size was a factor in the extinction of this ancient animal.



Fig. 177. Big antlers of a moose. (After Stone and Gram.)

That "fantastic deer," the giraffe, has a stubby pair of single antlers that are permanent, and remain in velvet throughout life (Fig. 68e).

The lateral prongs of the reindeer's antlers (Fig. 69A) are greatly flattened, serving as snow-shovels to aid these arctic dwellers in getting at the snow-covered "reindeer mosses" on which they feed in winter.

(c) **Pronghorns.** There are two species of ungulates with pronghorns. They are the pronghorn antelope, *Antilocapra americana* (Figs. 178 and 69F), and the "saiga antelope" of the Russian steppes, *Colus tatarica*, both of which possess permanent bony horns covered with a thimble-like sheath of horny integument that is periodically shed and renewed without the loss of the bony core.

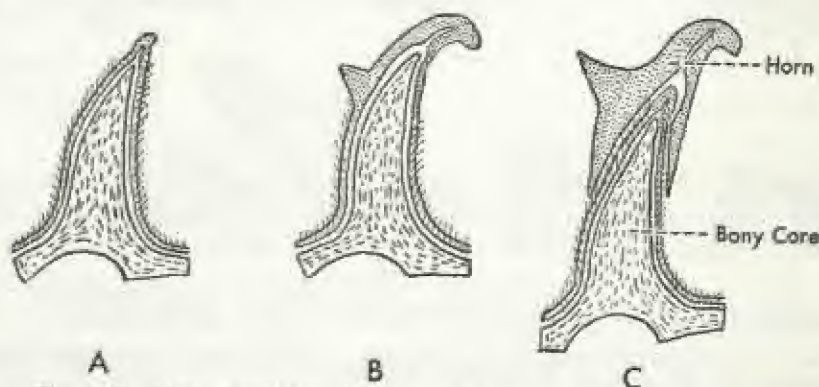


Fig. 178. Horn formation in the pronghorn antelope, *Antilocapra*. A, appearance shortly after shedding the cornified integumentary "thimble"; B, later stage with a new epidermal "thimble" forming with an extra prong; C, old thimble tip ready to be cast off, with new horny thimble already formed within. (After Nitsche.)

(d) **Hollow horns.** Finally, the most familiar kind of horns are the *hollow horns* of domestic and wild cattle, sheep, goats, and antelopes, which are usually present in both sexes.

Unlike pronghorns, hollow horns are not periodically shed. As the horn wears away it is renewed from the Malpighian layer of the epidermis, just as any other dead corneal structure is restored from within, the hollow corneal layer fitting over a core of living bone attached to the frontal region of the skull.

Hollow horns do not branch like antlers and pronghorns, but they assume a considerable variety of forms all the way from the majestic graceful spread characteristic of the Texas steer of the range, to the "cow with the crumpled horn." Polled, or hornless cattle were known long before cattle were domesticated by mankind, as shown by rude drawings of Palaeolithic polled cattle, depicted on the walls of prehistoric caverns of the cave dwellers in France and Spain.

4. Digital Tips

With the exception of the amphibians, the tips of the digits in those vertebrates that have fingers and toes are reinforced by hard integumentary structures, either claws, nails, or hoofs. Although amphibians do not have true claws, a thickening of the epidermal corneal layer at the ends of the

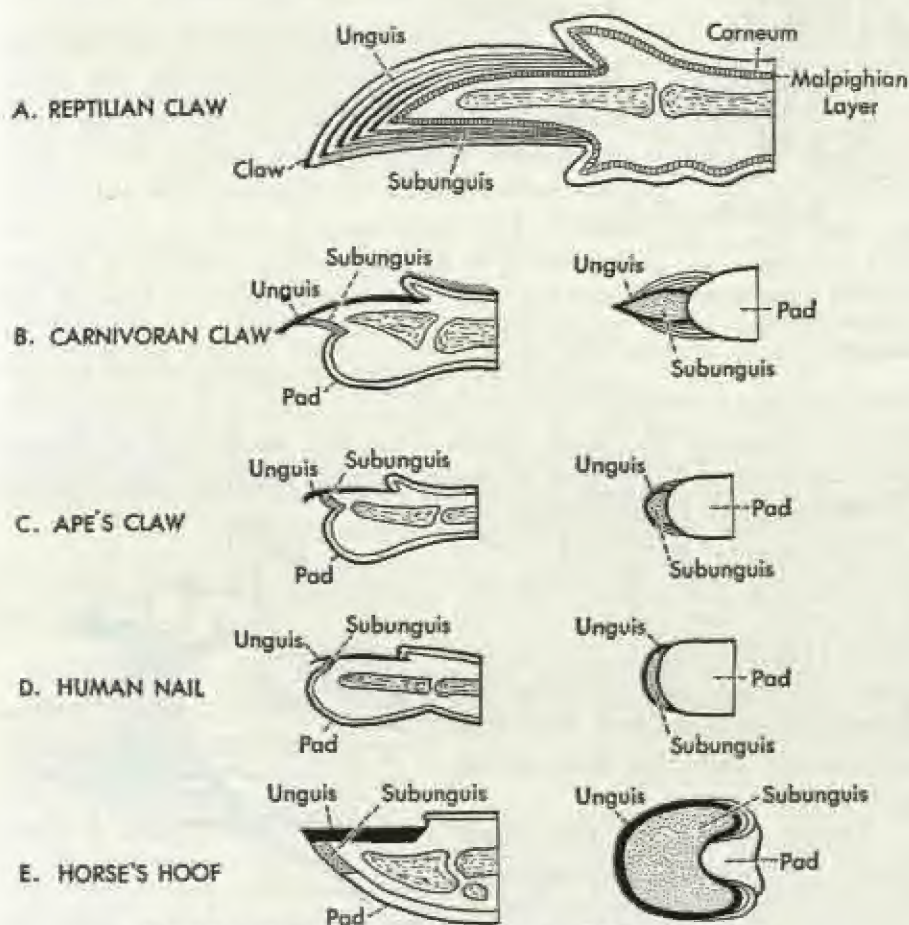


Fig. 179. Diagrams of hard digital tips. (After Bütschli.)

fingers and toes is a prophecy of claws to come later in the vertebrate series. In the African toad *Xenopus*, and the Japanese salamander *Onychodactylus*, these epidermal thickenings assume the definiteness of actual claws on some of the digits.

(a) **Claws.** The typical *claw of a reptile* (Fig. 179, A) may be regarded as being made up of two scalelike horny plates, dorsal and ventral,

so placed as to converge to a point at the end of the digit. The convex dorsal plate, *unguis*, is rounded in two directions, towards the tip and towards the lateral margins. The smaller ventral plate, *subunguis*, which is pinched in between the lateral edges of the *unguis*, is more flattened and of a less dense texture. Both structures are produced entirely by the Malpighian layer of the epidermis.



Fig. 180. Young hoactzin, *Opisthocomus*, climbing a tree by means of claws on wings. (After Lucas.)

In most cases the claws of birds are confined to the toes, although *Archaeopteryx*, the oldest known bird, had three finger-claws on each wing, while some existing types of running birds (*Ratitae*), have claws on the degenerate first and second fingers. The young hoactzin, of British Guiana, also has claws on its wings which enable it to venture from the nest and scramble about in trees on "all fours" like a lizard (Fig. 180)

In general pattern the claws of a bird are reptilian, although assuming a wide variety of forms adapted to correspondingly different functions. The sharp, slender claws of a woodpecker or chimney swift are designed for clinging to rough surfaces; the blunt stout claws of the domestic fowl for scratching; the hook-like talons of hawks and owls for grasping prey (Fig. 149); while the long straight claws of the Mexican jacana (Fig. 181), or the ends of elongated toes, enable this tropical species, in pursuit of its insect prey, to ski over unstable lily pads that float on the surface of the water.

Certain species of the grouse family (Tetraonidae) undergo a periodic ecdysis and renewal of the entire claw, a reminder of the changes undergone by other epidermal structures, such as the thimble-like caps on the horns of pronghorn antelopes, or the corneal layer of a snake's skin.

Mammalian claws cover the terminal bony phalanx of each digit. They consist (Fig. 179, n) of the *unguis* and *subunguis* of the reptilian claw, and in addition a terminal *pad*, or cushion, just behind the claw on the ventral



Fig. 181. Mexican jacana, *Parra*, with long straight claws which increase its ability to run over lily pads without sinking into the water. The male also has wing-spurs with which to fight. (After Plate.)

side of the digital tip. Since the animal bears its weight on these cushions, the corneal layer that clothes them is considerably thickened in consequence. Usually the dominant unguis becomes laterally compressed and curved down to a point, with the result that the subunguis is much reduced.

The claws of a cat are sharp and retractile within a protective sheath (Fig. 182), thus being kept unworn to be extended for use only in emergencies. The claws of a dog are less pointed and more exposed at all times, particularly so when it runs, for then they may come into contact with the ground, despite the presence of pads.

Bats and sloths (Fig. 65c) have claws developed into elongated hooks which, although making locomotion on the ground awkward and difficult, are very useful when these animals hang themselves upside down from branches in trees, as is their habit.

There are two striking modifications of mammalian claws, namely, hoofs and nails. In the first case the unguis thickens enormously into the shoelike *hoof*, which is so convex that its edges reach all the way around to the ventral side and come into contact with the ground. In the other case the unguis becomes flattened into the conspicuous *nail*, and the subunguis shrinks to a narrow insignificant rudiment under the projecting eaves of the nail, while the terminal pad becomes transformed into a sensitive ball, occupying the entire ventral aspect of the digital tip.



Fig. 183. Foot of an elephant showing separate hoof for each toe and a "rubber heel." (After Schmeil.)

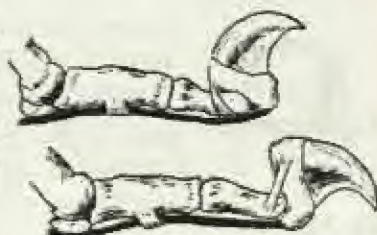


Fig. 182. Retractable claw of a cat. (After Hesse.)

(b) **Hoofs.** In a typical hoof (Fig. 179, E) such as that of a horse, the subunguis fills in ventrally the space between the lateral edges of the unguis, and the pad forms into a tough mass of material behind it, called the "frog," that serves somewhat the purpose of a rubber heel on a shoe. Hoofs, like the thick-soled shoes of a traffic policeman, are useful in supporting the heavy weight of the body in such animals as stand for long periods of time and so need a firm foundation to bear up their weight. The heavy elephant, which has a hoof on each toe, is particularly well provided with "rubber heels" (Fig. 183).

The surefootedness of hoofed animals, like the donkey and mountain goat, is in part due to the fact that the softer subunguis wears away faster

than the harder outer edge of the unguis, thus insuring a constantly well-shod foot with a sharp hard edge, in spite of destructive contact with rocky ground.

(c) **Nails.** Nails occur in man and other primates where they reinforce and protect the sensitive finger pads which play such an incalculable rôle in life. A person who attempts to pick up a pin, for example, with the fingers encased in gloves quickly realizes how much these structures can aid.

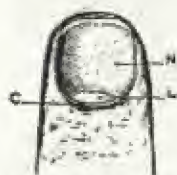


Fig. 184. Tip of finger. N, nail; L, lunula; C, corneum (eponychium) encroaching upon the nail at its base.

The human nail, which corresponds to the ungual part of the claw flattened out, is made up from closely compacted epidermal cells of the *stratum lucidum*, that is, the lifeless remains of what were once Malpighian cells. During its growth the distal part of the nail is continually advanced toward the tip of the finger or toe by additions from a thickened germinal matrix of Malpighian cells at its base, the position of which, particularly on the thumb, is marked by a white half moon, or *lunula* (Fig. 184).

The pinkish color of the nail, aside from the lunula, is due to its translucency which allows the blood beneath to show through. The lunula is white because the mass of Malpighian cells forming the nail-bed is so thick that the blood does not show through. Upon pressure the blood in the

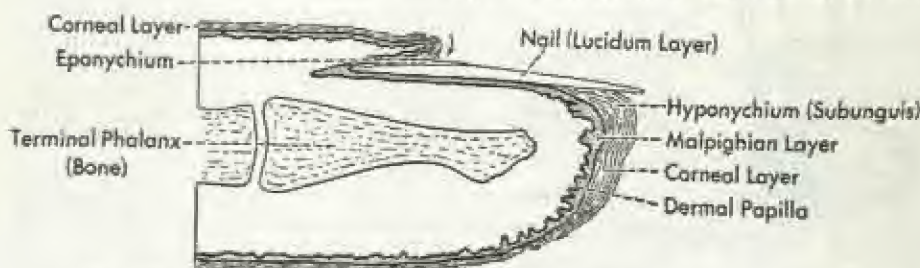


Fig. 185. Diagram of a longitudinal section through a finger tip, showing relation of epidermal layers to the nail, Malpighian cells are most active in the region of the lunula, indicated by small arrow. (After Bailey.)

underlying capillaries can be made to retreat, leaving the entire nail white like the lunula so long as the pressure is maintained. Transient white flecks sometimes appear in fingernails; due to accidental air-spaces imprisoned between the dead scalelike remains of the *stratum lucidum*.

The whole nail pushes out through a superficial corneal layer of the epidermis, leaving a ragged margin of corneum, the *eponychium* (Fig.

185), that may be seen encroaching upon the lunula and along the sides of the unguis. Under the free outer edge of the nail, where the continuity of the corneum is again broken, there is a narrow transitional region which is all that remains of the subunguis of the reptilian claw. Dirt collects here. The refinement of manicuring consists largely in attending to the ragged frame of corneum through which the nail projects.

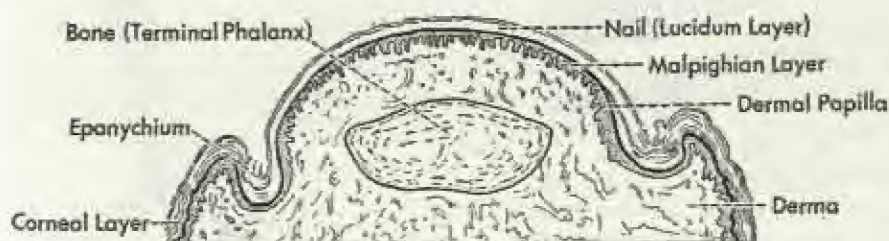


Fig. 186. Cross section through the finger tip of a child, showing relation of epidermal layers to nail. The eponychium is the part of the corneal layer that encroaches upon the nail. The stratum lucidum forms the nail. (After Lewis.)

The rate of growth of human nails is roughly an inch in six months, the rate varying with the general condition of health. A recent illness may be recorded by transverse depressions on the nails.

If human nails were never trimmed or broken, they ought theoretically to attain a length of over ten feet by the time one reaches the allotted age of three score years and ten.

In the human fetus the twenty nails first appear as terminal amphibian-like epidermal thickenings, at about the ninth week. By the twelfth week they are perfectly formed, but it is considerably later when they finally migrate into their dorsal position (Fig. 186).

The transition from the laterally compressed claws of most mammals to the flattened nails of primates is strikingly illustrated in certain lemurs which have claws on some of their digits and rounded nails on others (Fig. 187).



Fig. 187. Left foot of a lemur, *Perodicticus*, showing four nails and one claw. (After Huxley.)

5. Miscellaneous Corneal Structures

Many fishes have horny, epidermal, supporting rays, *actinotrichia* (Fig. 548) as well as bony or cartilaginous elements between the folds of skin that constitute the fins.

The rattle on the tail of a rattlesnake (Fig. 188) is a unique corneal

apparatus. Each time, as the snake molts the outer layer of epidermis, a button, or ring of cornium, remains behind to record the fact. These rings are dry and loose enough to make a rattling noise when the thrill felt by an excited snake reaches the tip of the tail.

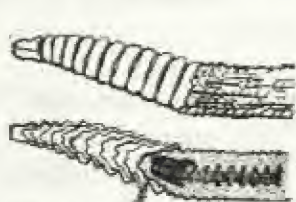


Fig. 188. The rattle of a rattlesnake, *Crotalus*, with eleven rattles. The lower figure is a long section, showing the vertebrae in black with the horny rattles fitting loosely one over the other. (After Garman.)



Fig. 189. Spur of a fighting cock.

Horny *beaks* are epidermal structures characteristic of the toothless turtles, birds, and monotremes. Among birds particularly they exhibit a great variety of form, and serve a wide range of uses.

Some male birds, such as game cocks for example, also develop horny *spurs* upon the legs with which they settle questions of supremacy upon the avian field of honor (Fig. 189). The male jacana that strikes at its rival with outspread wings is armed with effective *wing spurs* (Fig. 181).

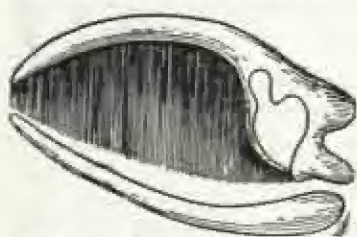


Fig. 190. Jaws of a whale, *Balaena*, with plates of "whalebone" hanging from upper jaw. (After Nuhn.)

The great sheets of "whalebone" (Fig. 190) with their frazzled edges that fill the mouth cavity of toothless whales, in the form of an elaborate mechanism for straining the myriads of small marine organisms upon which these giants feed, are not bone at all, but horny epidermal structures. Thick

at the base, each plate thins out rapidly and breaks up into a long fringe of slender, closely set processes like the teeth of giant combs.

Camels and dromedaries are provided with thick corneal *knee-pads* to protect these heavy animals when they collapse to a kneeling posture before lying down upon the sands. Similar though smaller corneal pads of less obvious function, called "*chestnuts*," are found on the inside of a horse's leg.

The astonishingly conspicuous crimson and lilac callosities upon the seats of such monkeys as the African mandrill are still another manifestation of the epidermis, serving these interesting animals, which sit much of the time perched precariously on the branches of trees, as peripatetic sofa cushions.

6. Feathers

Feathers are integumentary structures characteristic of birds. Strong, light, elastic, and waterproof, these extraordinary modifications of the epidermis are particularly fitted to the needs of animated aeroplanes. During the Jurassic Period, when, so far as is known, birds made their debut in the form of *Archaeopteryx* (Figs. 47 and 48), they were already clothed with unmistakable feathers. It is probable that these unique epidermal structures are homologous with reptilian scales, although evidence for this supposition is mostly embryological, since neither comparative anatomy nor palaeontology shows any unmistakable transitional structures between scales and feathers. The apparent scales on the flipper-like wings of the seagoing antarctic penguins are not true scales but instead are miniature flattened feathers, as a close examination at once reveals.



Fig. 191. A typical quill feather from a turkey. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

A typical feather (Fig. 191) is an elaboration of the lifeless corneal layer of the epidermis. Its *shaft*, hollow at the inserted end or *quill*, bears on its sides lateral *barbs* from which *barbules* extend. The barbules on the side of each barb farther from the quill bear *hooks*, like microscopic crochet hooks, which interlock with neighboring barbules (Fig. 192) forming a continuous expanse called the *vane*, that makes a fan-like surface resistant to air.

The germ of a *developing feather* appears as a papilla of dermal cells pushing the overlying epidermis up ahead of it. The base of the outgrowth, including derma and epidermal coat, gradually sinks into the skin (Fig. 193). There is thus a plug of dermal cells filling the epidermal covering,

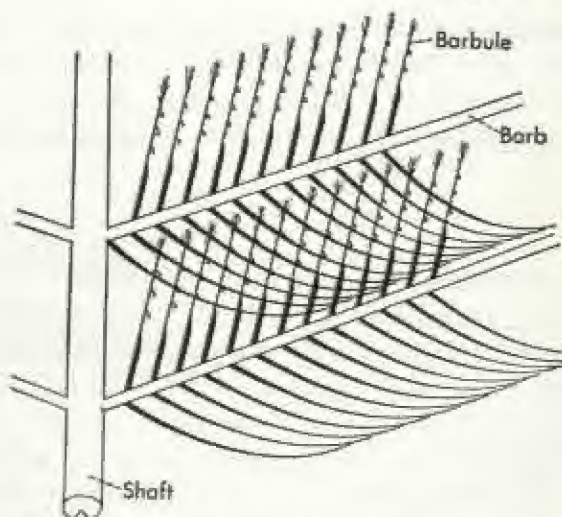


Fig. 192. Detail of a feather. (After Mascha.)

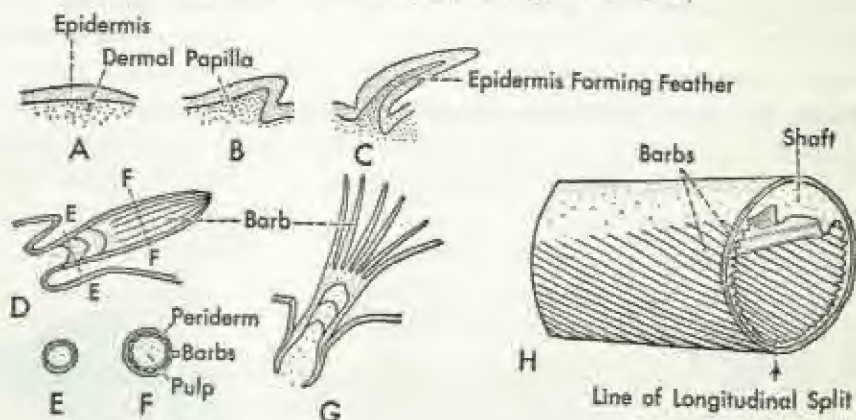


Fig. 193. Feather development. A, B, C, successive early stages, showing dermal papilla initiating development; D, later stage of a down feather cross sections of which, at levels E-E and F-F, are shown in E and F, respectively; G, a down feather, after rupture of periderm has permitted spreading of barbs; H, stereogram of part of a quill, or contour, feather. After periderm ruptures, germ splits lengthwise along lower side. The barbs, thus freed, spread upward and outward to form the vane.

but as the epidermis, hardening and cornifying, is pushed out from the papilla region, the dermal plug withdraws little by little, leaving a hollow lifeless quill inserted in the skin (Fig. 194). The embryonic feather is, therefore, at first a tube of cornified epidermis, set in a pit of the corium. Within the tubular embryonic feather the wall down one side is considerably thickened and later becomes the shaft from which the slanting barbs

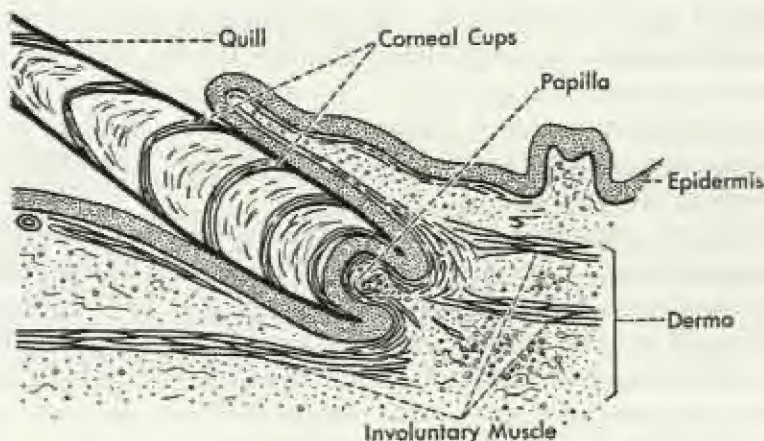


Fig. 194. Developing feather of a pigeon. The corneal cups are left in the quill by the periodic withdrawal of the papilla. (After Krause.)

of the developed feather extend on either side (Fig. 193). The wall of the tube opposite the shaft, the region of the distal tips of future barbs, is very thin. It is along this thin region that the rolled-up feather ruptures before it spreads out flat to assume its final definite form.

There are three general kinds of feathers, namely, *quill*, *down*, and *pin feathers*. Quill feathers may be further classified as *tail*, *wing*, and *contour feathers*, devoted respectively to the functions of steering, flying, and thatching. Tail and wing quills are larger and less flexible than the lighter and more delicate contour feathers that serve to fill out the unevennesses of the surface of the body, giving grace of curving outlines to the living bird. The part that contour feathers play in streamlining a bird is very apparent when one observes the scrawny body of a dead bird from which the feathers have been plucked.

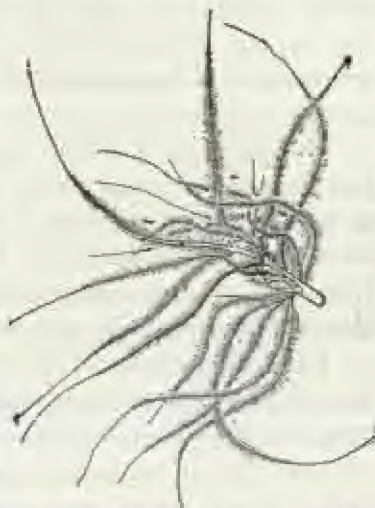


Fig. 195. A powder-down feather.

There are two kinds of down feathers, namely, *powder-down* (Fig. 195), and *nestling-down*. Powder-down feathers are characteristic of certain adult birds. They are interspersed and concealed among the contour feathers, and are more abundant on the breast and abdomen of herons

and birds of prey than elsewhere. The heat-retaining quality of powder-down feathers aids in the incubation of the eggs and the protection of the semi-naked nestlings. The shedding of powdery fragments, dropped from time to time, effects a sort of sanitary cleaning of the plumage of birds whose nests are particularly liable to become daubed with excreta and the remains of animal food.

Pin feathers, although superficially resembling hairs, are complementary in structure to down feathers. They have practically no barbs, consisting instead almost entirely of the shaft which is missing in down feathers that are made up of barbs and barbules. Pin feathers are scattered quite generally over the body among the contour feathers, although in certain birds, such as flycatchers and whip-poor-wills, they become localized about the mouth opening, serving as a "barbed wire" entanglement in the capture of insects on the wing. In common use, the term pin feather is also applied to the young quill feathers present, in addition to true pin feathers, after the so-called plucking of the bird.

In a quill feather interlocking of the barbules occurs only in the exposed part of the vane which is not overlapped by other feathers. During the effective downward stroke of the wing in flight, the vanes of neighboring feathers close up together, presenting to the air a common continuous impervious surface, while upon the return upstroke they separate somewhat, thus letting the air through with less resistance. An entirely different irregular arrangement is characteristic of down feathers and pin feathers, which have nothing to do with locomotion.

The *plumage* of a bird consists of all the feathers taken together. The *first plumage* of young birds is the transient nestling-down, which appears as fluffy tufts on the tips of the emerging contour feathers. In this first plumage it is the tip of the epidermal tube that frays out like a brush (Fig. 193) to form the nestling-down feather, which is fated to wear off after temporary service and be replaced by the unfolding quill feathers.

The nestling-down of the first plumage is thus replaced by the so-called *juvenile plumage*, which is made up of the first coat of true quill feathers. This lasts the young bird through its first winter when, in most cases, it is replaced by the *nuptial plumage* that heralds the first love affair in the spring. In the following autumn, after the adventure of raising the first family has been accomplished, the nuptial plumage, now faded and shabby, is exchanged for a *post-nuptial plumage*. Every year thereafter that the bird lives there is a new post-nuptial plumage after the breeding season and in the case of many birds an additional nuptial plumage in the spring.

This process of ecdysis by means of which one coat of feathers is

exchanged for another is called *molting*. When a dead feather loosens from its socket in the skin and is lost in molting, the living epidermal Malpighian cells at the bottom of the pit, backed up by nutritive resources of the blood vessels from the underlying corium, grow out into a new embryonic feather tube, which in turn unrolls to take the place of the dead feather that was lost.

Water birds, gallinaceous birds, and some birds of prey are said to be *precocial*, because at hatching they are quite well clothed with nestling-down, while certain other birds, such as kingfishers and woodpeckers, are described as *altricial*, because they are hatched almost naked, only subsequently acquiring their first coat of feathers.

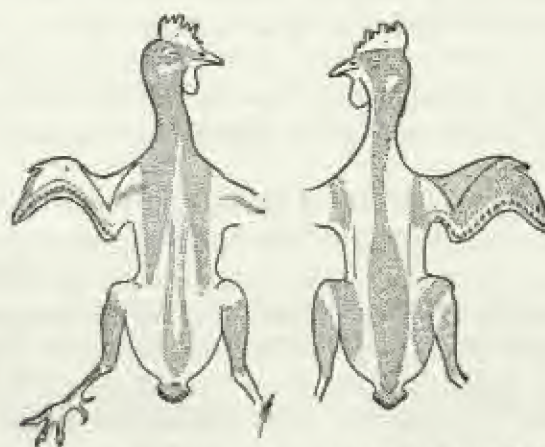


Fig. 196 *Pterylae*, or feather tracts, on the body of a cock. Ventral view at the left, dorsal at the right. (After Nitsche.)

Although the feather coat forms a remarkably complete covering over the body, the insertion of individual feathers in the skin is by no means equally spaced. Feathers are attached in localized patches called *pterylae* (Fig. 196), between which there are naked areas, *apteria*, covered by overlapping feathers from neighboring *pterylae*. No doubt *apteria* in such areas as the "armpits" and the inguinal region facilitate freedom of locomotion in much the same way as do loose running trunks on the legs of a sprinter. *Apteria* on the abdomen of a bird may also be useful during incubation, because the eggs are thereby snuggled into more direct contact with the warm body of the brooding mother.

The constancy and orderly arrangement of the various *pterylae* has been used by systematists in determining the relationships of different kinds of birds for purposes of classification. Ostriches, toucans, and modern penguins are apparently exceptional in that they do not in adult life show a pattern

of feathers in pterylae and apteria. That this is a secondary acquisition and not a primary condition is indicated by the fact that fossil (Tertiary) penguins, and embryonic ostriches, show distinct pterylae.

Local deviations in feather arrangements, usually associated with secondary sexual characters, are of frequent occurrence, such as the crests and ruffs of various birds, and the spectacular tails of peacocks, fantail pigeons, and lyre birds. In a strain of fancy poultry known as "frizzles," the plumage has departed from nature's approved style by reason of the twisting of the feather shafts, but it is doubtful whether these curious frowzy birds could successfully maintain themselves out of domestication.

The shingle-like *lay of the feathers* is directed from the head toward the tail, thus reducing to a minimum the air resistance offered by the plumage. This orientation of the feathers also makes possible the retention under the feathers of a layer of warmed air next to the skin during rapid flight, which would be blown away if the feathers were arranged in any other fashion.

The remarkably varied *colors of feathers* are due to one or both of two factors, namely, chemical pigments and the physical arrangement of the elements making up the feathers. The reds, yellows, and blacks are due to pigments. The whites, blues, and iridescent colors are structural colors. The greens are usually due to a structural blue combined with a pigment yellow.

Pigments are deposited mostly in the exposed parts of feathers and only during the period of their growth. After feathers have become differentiated lifeless structures there is no way to add pigment granules to them, so that further change in color of plumage can then only occur in one of three ways, by fading of the pigment already in the feathers, by the wearing away of the particolored feather tips, or by complete ecdysis of old feathers and their replacement by new ones.

A feather appears white if no pigment is present and the polygonal cells of the barbs and barbules break up the light and reflect all wave lengths equally.

The blue color of feathers is of the type known as Tyndall blue. Many years ago Tyndall showed that the sky appears blue because minute suspended particles of dust, water, and the like scatter the short, blue waves of light while permitting the longer, red waves to pass through. Therefore, when we see light reflected from these particles or from similar suspended particles in any turbid medium (e.g., skimmed milk), we see the blue wave lengths. On the other hand, if we look at the turbid medium using only light which is transmitted through it, the material appears reddish because the short, blue waves have been scattered and the longer, red waves trans-

mitted. The blue color of feathers is localized in the layer of cells which is just beneath the outer sheath of the barbs. Minute pores in the walls of these cells bring about the scattering of the blue wave lengths while transmitting the longer ones. As we ordinarily see feathers by reflected light, any area which brings about this scattering will appear blue.

In almost every case green feathers exhibit the same structural features as blue ones but have, in addition, a yellow pigment in the outer sheath of the barbs, the combination of the two colors producing green. A green copper pigment has, however, been extracted from the feathers of the West African "turacou," *Turacus*.

Frequently contour feathers present complicated variegations of colors which combine to form *patterns*, involving the matching of parts of several neighboring feathers. Thus, a white wing-bar, or a spot on the breast, is in reality a baffling mosaic, made up of unequal fragmentary contributions of color from many separate overlapping feathers, which have grown independently into harmonious positions with relation to each other. No wonder that Darwin is said to have exclaimed that trying to think out how the "eye" on the dorsal feathers that constitute the peacock's tail came about, *made him actually sick!*

In the process of molting, feathers in the centers of the separate pterylic are the first to fall out, and this loss with its subsequent replacement extends from these centers to the margins of the different feather islands.

Sometimes a molt is incomplete not involving each feather, but simply the wearing away of a different colored tip. This may be quite effective, however, in accomplishing a change in general appearance, as for example, in the case of the male bobolink, *Dolichonyx*, which changes from a distinctive coat of black and buff in patches of color in the spring to an inconspicuous streaked sparrow-like plumage in the fall.

7. Hair

Just as feathers characterize birds, so hairs are integumental hall-marks of mammals. Such apparently hairless animals as whales and sea-cows even are clothed in part before birth with embryonic hair, while the bare thick-skinned rhinoceros and the hippopotamus have sparse bristly hairs about the snout, and the big, apparently naked elephant, whose skin upon close examination is about as forbidding as a chestnut burr, has a supplementary mammalian passport in the form of a tuft of hair at the end of its ridiculous tail.

Hair serves a variety of uses besides its obvious benefit of affording general protection. The air-imprisoning pelt of a fur-bearing animal retains

the bodily heat and sheds the rain; the thick mane of a wild horse is a specially placed buffer against carnivorous enemies that would pounce



Fig. 197. Vibrissae of a cat. They form a sensory halo that determines a hole large enough for the body of the cat to pass through.

upon its otherwise unprotected neck; the squirrel's frisky tail is a portable blanket which conveniently enwraps the owner when at rest; the anteater's bushy tail is a diverting and confusing barrier to the armies of ants that swarm forth in defense when the anteater makes a foray upon their citadel; the long hairs of the horse's tail form an effective brush to ward off pestering insects; the stiff sinus hairs, or *vibrissae*, that supply the snouts of many mammals, are sensitive "feelers" (Fig. 197); and lastly, the color schemes carried out on the bodies of mammals, whatever uses they may serve, are due principally to hairs

as color bearers. Transient sinus hairs on the inner or contact side of the forearm in the human embryo (Fig. 198) hark back to arboreal lemur-like life.

In structure a single hair (Fig. 158) is an epidermal shaft projecting, usually at an acute angle like an exaggerated leaning tower of Pisa, from a pit or depression in the skin. The projecting dead part of the shaft is typically cylindrical, with the root concealed at the base in the pit expanding into a club-shaped *bulb* that derives nourishment from the corium through the living Malpighian cells producing it from below. Directly beneath the bulb and in intimate contact with it, is an upward-projecting *dermal papilla* containing capillaries and nerve endings which supply the hair root. Corneal cells, surrounding the root of the hair, constitute the *inner root sheath*. Other epidermal cells that form the *outer root sheath* line the walls of the pit. The root of the hair with its sheaths make up the *hair follicle*.

Opening into the pit from the sides are sebaceous glands, which produce an oily secretion that renders the dead hair shaft less dry and brittle.

In cross section a hair shaft ordinarily shows three kinds of cells, namely, those of an inside core, or *medulla* (absent in human body hair); a surrounding ring, the *cortex*, making up the bulk of the hair; and a thin outer single layer of shingling cells, the *cuticle*.

Although the root of the hair may be embedded deep in the corium, the entire structure is epidermal in origin except the papilla, which is dermal.



Fig. 198. Transient sensitive hairs on the inner, or contact side, of the fore-arm in a human embryo. (After Broman.)

The shaft of the hair usually tapers towards the tip and does not branch, although bristles sometimes split distally. Frequently hairs taper also towards the root end, particularly near the point where they emerge from the skin, so that they tend to bend easily when stiff or give way instead of breaking off upon contact with external objects. The exquisite softness of the fur upon a mole skin when it is stroked either way is due to this adaptation of hairs thinned down at the surface of the skin, which enables the animal to go forward or backward in its burrow with a minimum of frictional injury to the pelt.

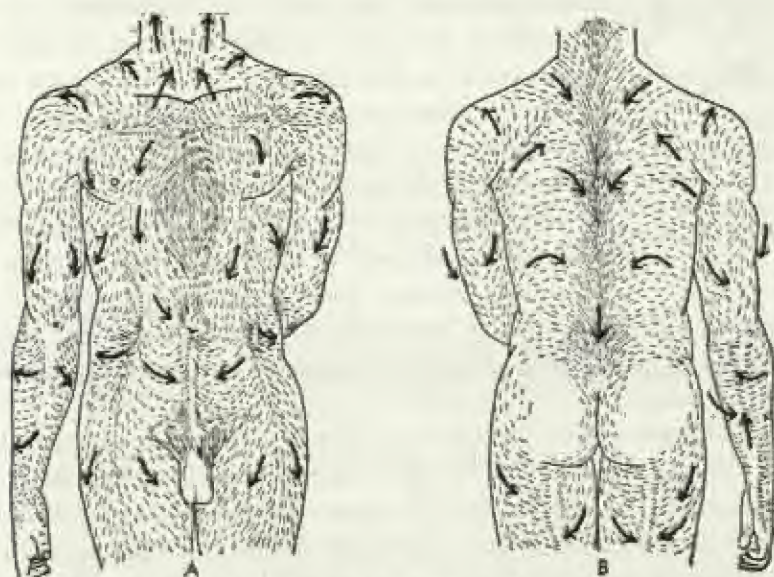


Fig. 199. Diagram showing, A, the more usual hair currents upon the front or ventral aspect of the trunk, and B, on the back or dorsal aspect of the trunk. (After Kidd.)

Each follicle is supplied with an involuntary muscle, *arrector pili*, running from near its base diagonally to the superficial region of the corium, on the side towards which the hair slants. When this smooth muscle shortens, it pulls upon the base of the follicle causing the hair to "stand on end" (Fig. 158). The action of the *arrectores pilorum* is particularly noticeable upon the scruff of an angry dog's neck, or upon the tail of a frightened cat, when these animals take on a more terrifying aspect as the result of this reflex. The ghostly remains of this apparatus in man is the cause of "goose flesh," which appears when the skin contracts somewhat upon exposure to cold. "Then a spirit passed before my face; the hair of my flesh stood up." (Job 4:15.)

The slant at which hairs emerge from the skin varies in such a way that in their direction the hairs taken together form *vortices* and *streams* as they lie over the surface of the body (Fig. 199). This is particularly apparent on a horse or short-haired dog.

Convergent vortices form around the base of projecting structures, such as horns, the tail, and the umbilical cord. These hair whirlpools persist even after the structure around which they converge has disappeared, for example in man about the umbilicus, and at the focus in the coccygeal region where the vanished embryonic tail was formerly located (Fig. 200).



Fig. 200. Tuft of coccygeal hairs on a human embryo suggesting an ancestral tail. (After Ecker.)

Perhaps the most familiar instance of *divergent whirlpools* is on the human scalp at the vertex of the crown, where the hairs are centrifugally arranged. Other divergent vortices appear in the axillae. The coarse hair of the sloth is divergently parted along the midline of the belly instead of down the back as in most mammals. This adaptation, as in other divergent streams and whirlpools wherever found, is useful for shedding rain.

The unusual arrangement in the case of the sloth is due to the fact that this mammal customarily hangs suspended upside down from the horizontal branches of trees.

Although hairs are not arranged in definite patches like the pterylae of feathers, they do emerge from the skin embryonically in orderly array with reference to each other (Fig. 201). In man they appear in groups of twos, threes, and fours with the largest hairs in the middle of each row, these rows in turn being spaced in such a way as to suggest that each one is homologous with an interscale area. This hypothesis is further borne out by the arrangement of hairs in similar groups in other mammalian skins, particularly those of the armadillo and scaly anteater where scales are actually present with a definite group of hairs behind each scale.

In mammals other than man, localized masses of hair appear as fetlocks, tufts, manes, and modifications of the tail. A horse is enabled to brush away annoying flies with a "swish" of long hairs on the tail, while a cow accomplishes the same result, as every farm boy who has ever milked a cow knows, with a "flip" of the terminal tassel.

Hairs occur in various shapes and forms all the way from hard rigid *spines*, like those of the porcupine, European hedgehog, spiny mouse, and spiny anteater, to the soft delicate *wool* of sheep and goats. The *bristles* of swine are stiff elastic hairs, sometimes with split ends, in which the outer layer of cuticle predominates. They are more numerous on the dorsal side of

a hog than elsewhere on the body and tend to make the wild animal look somewhat larger and more formidable.

Fur is composed of dense soft hairs, frequently lacking the medulla, with a few long coarser hairs interspersed. In the process of transferring the skin of a seal to milady's back in the form of a sealskin coat, the long stiffer *guard hairs* are carefully removed, leaving the soft thick-set *fur-hairs* making a uniform surface.

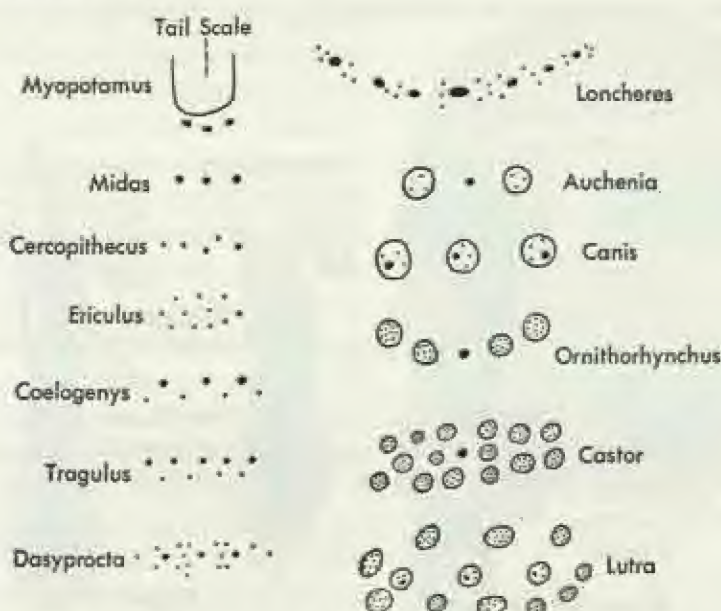


Fig. 201. Hair groups of different mammals. (After Meijere.)

The cuticle of *wool hairs* is usually rough and scaly, and since the hair shafts are somewhat twisted they spin well into yarn because the separate hairs interlock easily.

Sinus hairs, or "feelers" (Fig. 197), that radiate from the inquisitive noses of nocturnal prowlers, such as cats, rats, and weasels, are each seated in a large papilla especially well provided with nerve endings, so that any chance contact which disturbs the stiff outstanding dead shaft is communicated at once to sensory headquarters through the mechanical agitation of the basal papilla.

The unusual beard on the faces of goats and men is the very latest evolutionary style in hair decoration. That the human beard is not so much a relic of the past as a prophecy of the future, is evident not only by its sharp differentiation in the male sex, and its delayed appearance in the individual, but also by the fact that it is much less apparent in the more primitive races.

Sexual differentiation of human hair is largely controlled by hormone action as demonstrated when sexual hormones are prevented from normal occurrence by the removal of ovaries or testes. The distribution of adult female hair over the body is intermediate between that of the embryonic or infantile condition and the arrangement in the adult male.

Although man is one of the least hairy of the mammals, with the exception of the aberrant whales and sea-cows, an examination of his embryonic development shows his close relationship to other members of the order of Primates.

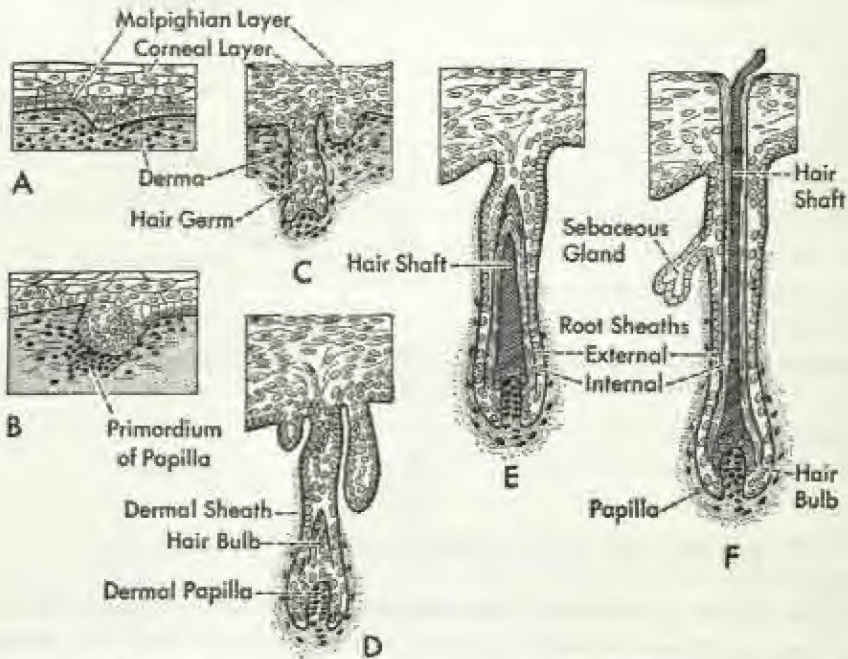


Fig. 202. Six stages in the development of a hair. A and B, from embryo of a sheep. (After Schimkewitsch.) C and D, from a mole. (After Maurer.) E and F, from human embryo. (After Hertwig.)

The first evidence of hairs in the mammalian skin is found in the form of concentrations of epidermal cells which, because of displacement resulting from their rapid multiplication, grow down like plugs into the corium (Fig. 202), and become hair follicles. The bulb of each follicle, with its surrounding inner and outer root sheaths, soon differentiates, and the newly formed lengthening shaft pushes out towards the surface, loosening the temporary epitrichium which at this stage covers the body like a gauzy envelope. The hairs in man first emerge at about the fifth fetal month, in

the region of the forehead and eyebrows, eventually becoming a transient coat of delicate embryonic fur called *lanugo* (Fig. 203), which clothes the entire body with the exception of the lips, palms, soles, nails, and spaces around the apertures of the external genitalia. The lanugo usually reaches its highest development during the eighth fetal month, when it begins to be shed into the amnionic fluid that surrounds the embryo, and is replaced by the permanent hair, at least over certain parts of the body. It remains longest on the shoulders and in many instances is still in evidence at birth.

The permanent hair in attaining its growth becomes localized in distribution, and differentiated for various uses, as already pointed out. It is thickest on the top of the scalp, since it was originally adapted to shed the rain which fell alike on our just and unjust hatless arboreal ancestors. In apes, which assume a semi-erect posture with the crown of the head projecting somewhat forward instead of upward, the hair, as would be expected, is thicker on the scruff of the neck than on the top of the head.



Fig. 203. Face of an embryo five months old with *lanugo*, or temporary hair covering. (After-Ecker.)

Hairs are also conspicuously specialized in man in the form of eyebrows, eyelashes, and as guardians of nasal and external ear passages against dust invasion. At the pubes and axillae cushions of hair that perhaps tend to lessen friction develop at puberty, while the remainder of the human body, which normally appears to be comparatively bare, is supplied in varying degree with hairy reminders of other days.

Hairs of the head are *straight*, *wavy*, *curly*, or *kinky*. In cross section the series varies from nearly round in the straight head hair of Indians and Mongolians, to elliptical in the kinky hair of the Hottentot. The shaft of curly or kinky hair, growing more rapidly on one side than on the other, emerges from the skin in a curve. Pubic and axillary hairs usually curl, even in straight-haired people, and straight hair tends to curl in wet weather while curly hair tends to straighten. True "permanent waves," like poets, are born not made.

Growth of hair varies individually, in health and sickness, seasonally,

with quantity and quality of food, with climate, and with the region of the body on which it occurs. The beard hairs may easily grow a millimeter in twenty-four hours. Dr. W. W. Keen reckoned that with the production per millimeter of approximately 500 cells of hair, there would need to be only 5000 hairs on the head to produce 40,000 hair cells per minute. This is what keeps barbers busy.

According to the *manner of growth*, hair is either *definitive* or *angora* in character. Definitive hair grows until a certain length is attained, when it becomes pinched off from its base of supplies in the papilla of the bulb (Fig. 204), and the lifeless hair shaft loosens and is shed. A new hair then starts to grow. The interruption in growth at the root of an angora hair does not occur either as often or as completely as in definitive hair, so that the shaft continues to lengthen as long as the follicle remains intact. In man the body hairs are definitive, while those of the scalp are angora in character. In apes those of the scalp are also definitive.

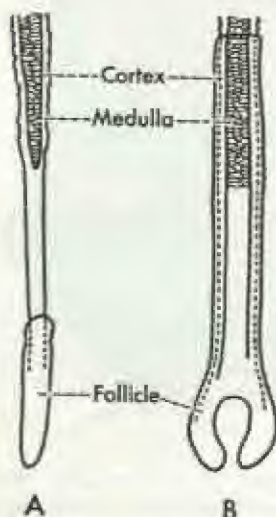


Fig. 204. A, base of hair, fully grown, of definitive growth type. B, base of angora hair of indefinite growth type. (After Castle and Forbes.)

The *color* of hair is due to pigment deposited during growth in the intercellular spaces of the cortex. When hairs "turn gray" there is a reduction in the amount of pigment present and an increase in the number and size of the light-reflecting air-spaces between the cells. Gray hair in man appears first at the "temples," situated over the temporal bones, so-called because here the flight of time is marked. In dogs the graying of hair usually begins on the snout, while in mice and rats it may be anywhere on the body. Some animals

such as the varying hare, *Lepus americanus*, for example, show a seasonal whitening of the hair coat, that brings them into harmony with their snowy habitat, thus insuring them a degree of protection against their enemies.

Data on particular differences in human hair have been gathered in certain cases. For instance the head hair of blondes is usually finer, longer and more dense than that of brunettes. Someone has made an estimated census, after a partial count, of the number of head hairs on four females with the following result: blonde, 140,000; brown, 109,000; black, 102,000; red, 88,000. A mathematical moment with a pencil and a pad of paper reveals the fact that if the blonde lady in question should have her

hair bobbed, supposing that it was originally two feet long, she might thereby dispose of something over fifty linear miles of hair.

Ecdysis, or molting, which is so universal a phenomenon of other epidermal structures, occurs at intervals also in the hair coat. With most mammals shedding the hair is more pronounced in spring and early summer than at other seasons, but with man it is a continuous process, involving a normal daily loss which may be increased under pathological conditions. A single head hair, according to Lewis, ordinarily lasts from four to five years, while eyelashes are normally replaced in as many months. Failure in the replacement of hairs of the scalp results in baldness of which there are two general types, both evidently hereditary. In one the divergent whirlpool of hair about the vertex of the crown is the first to go, when the subject comes to resemble a tonsured monk. In the other case the hair retreats from the forehead with the passing of the years, leaving an increasing expanse of apparent intellectuality. When both types of baldness descend upon the same individual the polished dome of the skull may be as bereft of hair as a billiard ball. Baldness, even if the truth be told, is very much more common in men than in women.

Under pathological conditions, unusual abundance of hair, *hypertrichosis*, or abnormal absence of hair, *atrachosis*, may occur. The latter condition is frequently associated with defective development of the teeth.

When embryonic lanugo persists it is spoken of as *pseudo-hypertrichosis*, as distinguished from *hypertrichosis vera*. The latter is exemplified by the presence of superfluous hair in the case of bearded women and shaggy men.

8. Friction Ridges

Upon the tips of human fingers one can easily see with the naked eye peculiar fine ridges, called *friction ridges* because they aid to a certain extent in preventing the fingers from slipping when brought into contact with objects. They are arranged mostly at right angles to the direction in which there is the greatest tendency to slip. Sweat glands that open upon them, like craters along the peaks of tiny volcanic mountain chains (Fig. 139), provide moisture, bringing about much the same result as when a workman "spits on his hands" to secure a better grasp.

Since friction ridges appear only on those areas that come habitually into contact with objects, they are particularly developed on the palmar and plantar surfaces of the hands and feet of man and other primates, and also on the concave side of the prehensile tail of the long-tailed American monkeys (Fig. 205). They are absent from the middle of the back, fore-

head, and rim of the ear, and other regions not employed in taking hold of things.

A histological examination reveals the fact that the ridges and furrows of the epidermis in the friction areas match corresponding downgrowths into the underlying derma. Furrows between papillary ridges should not be confused with the many wrinkles and folds that beset the skin all over the body.



Fig. 205. Prehensile tail of a monkey, *Ateles*, showing friction ridges in region of contact. (After *Journal of Heredity*, April, 1918.)

Friction areas are particularly associated with padlike epidermal elevations, or *tori*, that originally appear on the palms and soles. Typically there are ten of these elevated tori on each hand or foot, namely, five *digital areas* forming the balls of the fingers and toes; three *interdigital areas* on the palm or sole near the base of the digits; one *thenar*; and one *hypothenar area* at the posterior part of the palm or sole on the side of the big digit and the little digit respectively (Fig. 206). Although present as distinct elevations throughout life on the feet of certain mammals, the mouse for example, and also on the hands and feet of the

human embryo, tori as such disappear in adult man, since, as the human embryo grows older, these elevations or pads become less pronounced and are eventually flattened to form the friction areas.

The various minute patterns which the ridges of the friction areas assume are all definitely established before birth and retain their individ-

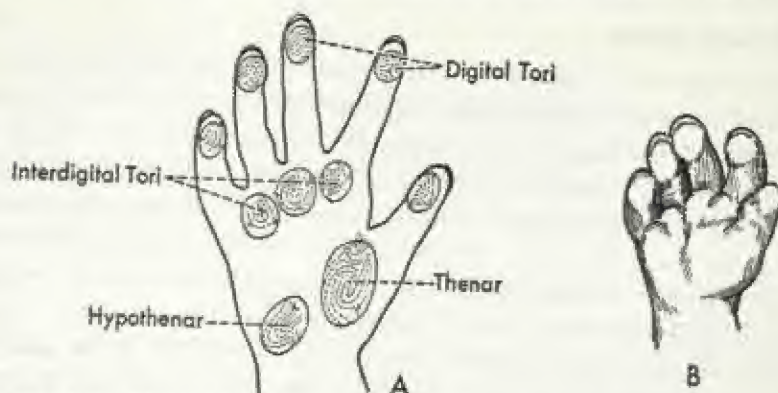


Fig. 206. Arrangement of the *tori*, or elevations which become the friction areas on the palmar surface of the hand. A, diagram of typical arrangement. (After Wilder.) B, hand of a human embryo of 22 mm in which corresponding tori are seen. (After Retzius.)

uality, except for slight increase in size, throughout life. It has been demonstrated that when friction ridge patterns are destroyed by searing or by sandpapering the finger tips, the old patterns are restored upon subsequent growth of new epidermis.

Since the details of the patterns are unlike, not only in different persons but also on the twenty fingers and toes of the same person, they furnish an excellent means for personal identification. Just as primitive peoples in the past have frequently employed indelible tattoo marks in order to distinguish themselves from their fellows, so friction ridge patterns, which have been called "nature's tattoo marks," are made to serve a like purpose.



Fig. 207. Diagrams of the four main types of finger patterns. The whorl and the composite have *two* deltas (Δ 's); the loop, *one*, and the arch, *none*. The loop may be a *radial* loop, or an *ulnar* loop according to whether it opens outward toward the thumb (radial), or toward the little finger (ulnar.) (After Wilder and Wentworth.)

The patterns may be roughly classified in general types, namely, *whorls*, *loops*, *composites*, and *arches*, as indicated in Figure 207. Loops may be *ulnar* or *radial* according to whether they stream outward toward the ulnar (little finger) or the radial (thumb) side, while arches may be *simple*, as in the figure, or if more pronounced, *tented arches*. Combinations of these types upon the fingers of both hands taken together, and the infinite variety in the minutiae that each type reveals upon careful scrutiny, make possible an almost unlimited subdivision and classification. Thus, it has come about that finger-print codes have been worked out, which may even be telegraphed or radioed from one part of the world to another in the interests of personal identification.

By reason of the fact that finger prints are easily made and kept on file, they may be utilized conveniently in a great variety of ways. Upon a bank cheque, passport, or non-transferrable documents of any kind, for example, such a personal imprint furnishes a unique signature which cannot be forged. In the case of soldiers, sailors, the personnel of large industrial plants, voters, babies at maternity hospitals, inmates of institutions, criminals, undesirable immigrants once rejected, dead bodies recovered from disastrous catastrophes or accidents, aphasia victims, and in many other

instances, finger prints offer a simple and invaluable means of establishing identity (Fig. 208).

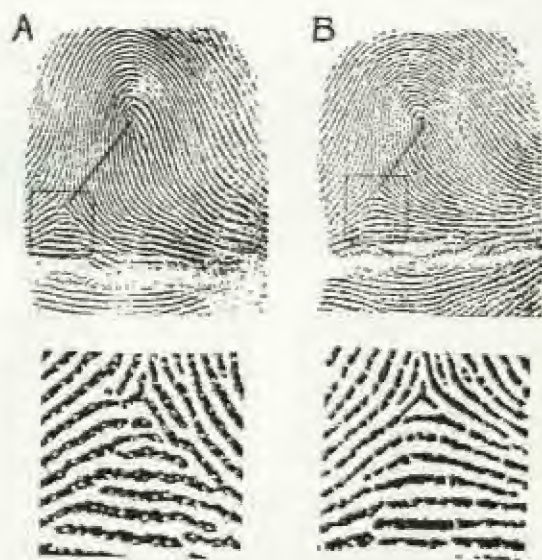


Fig. 208. Two sets of finger prints, superficially alike but quite different in detail. A, print of the middle-right finger of J. C. (Magnified two diameters.) The area enclosed in the square is shown below in an enlargement of 11 diameters. B, print of the right middle finger of J. W. (Magnified two diameters.) This was selected from several hundred prints of middle right fingers in the endeavor to get the nearest match to A. The corresponding enlarged square below shows distinct differences that are not evident upon superficial examination. (From Wilder and Wentworth.)

Since Galton's pioneer work in England,* and the appearance of Mark Twain's whimsical classic,† in which the imagination of the story teller anticipated the later applications of science, the serious study and utilization of the ineffaceable friction ridges has developed into a real science by itself (*Dactyloscopy*) with a considerable and growing bibliography. It is now known that two widely separated peoples, the Chinese and the Babylonians, in very early times made use of finger-print signatures.

* *Finger Prints*, 1892.

† *The Tragedy of Pudd'nhead Wilson*, 1894.

Intake Apparatus-Digestive System

I. IN GENERAL

1. The Whirlpool of Life

Life is manifested as a process of release of energy, involving continuous death or destruction, since it is only by the breakdown of cells and tissues in which energy from food has been stored that the phenomenon of life can appear or continue. Thus, the paradox that we live by dying. There is, however, more than one kind of death. The kind referred to in this connection is the *local death* of cells and tissues, which is usually accompanied by regeneration and recovery, while what may be called *general death* is that in which the correlation of functions depending upon the brain, heart, and lungs is interrupted so that it cannot again be resumed. Even in this latter case the component tissues may live on for some time after correlation is no longer possible, as shown, for example, by the excitability of the muscles of a frog's leg under electrical stimulation after the frog has been irrevocably killed by the complete removal of its brain and heart.

Huxley likened an organism to the whirlpool below Niagara Falls. At no two moments of time is it made up of the same mass of water, yet its identity remains, and if photographed on succeeding days from the same point, the pictures would appear alike. In a similar manner all living things may be conceived as whirlpools of living matter and energy, which nevertheless maintain a continuous individuality throughout the duration of life.

The digestive system is the mechanism that makes good the constant losses which are inevitable in the mortal expense of living. It is with the intake aspects of the organic whirlpool that this chapter is concerned.

2. Rate of Living

The rate at which the metabolic waters of life flow through the organic whirlpool varies greatly with the age of the individual. During the first part of life while growth is taking place, the intake, like a spring freshet,

is greatly in excess of the outgo, but later there follows a prolonged period of balance during which losses of energy are simply made good, then the stream of life flows more slowly and becomes less and less in volume, and eventually ceases entirely as the head waters gradually dry up.

It is not at all easy to realize the abounding life of animals during the onset of growth. A human baby normally doubles its weight in 200 days. A new-born mouse quadruples its weight in twenty-four hours, and a silkworm increases its size 500 times during the first day's intake of mulberry leaves. Dr. Keen says: "Were the same rule to hold, a baby weighing seven pounds at birth would weigh thirty-five hundred pounds the very next day, and when a month old would weigh one hundred and five thousand pounds, or over fifty 'short tons,' which, however, could hardly be called 'short weight.' "

3. Hunger and Thirst

Food, water, and oxygen are the necessary materials of subsistence taken into a going organism. Food carries energy to be stored up in the tissues for later use. Water is the universal solvent and fluid necessary for manipulating and shifting about materials within the organism, while oxygen effects the breakdown of tissues and the liberation of imprisoned energy.

The essential concern of every animal is the securing of these three primary prerequisites for continued activity. This fact is so obvious that it escapes our attention. Anyone who has tried to follow the incessant activities of a wild bird, for example, during the daylight hours will realize in part the imperious demands of hunger and thirst. It may be observed that most animals rarely succeed in overtaking their appetites.

Even in the highly specialized routine of human society, the daily program of business, pleasure, education, religious activities, politics, philanthropy, and all the rest, is secondarily tucked in between meals around which the day's activities are arranged, and any serious deviation from the periodic exercise of the *sacred rites of intake* are likely to border on the disastrous.

4. The Intake Mechanism of Animals and Plants Contrasted

Most plants are restricted to a diet. The food they use is monotonous in the extreme, yet there is no complaint. It is made up in the synthetic laboratories of the green cells of leaves or stem out of uniformly distributed raw materials, such as carbon dioxide and oxygen from the air, and water impregnated with dissolved salts of the soil.

Liquid intake from soil-water is soaked up by osmosis through the delicate walls of *root hairs* (Fig. 209), which would quickly collapse if exposed to dry air. This does not ordinarily happen, however, as root hairs remain constantly protected in damp soil, since the plant is not forced to travel about seeking water and what it may devour.

Animals, on the other hand, do not have the power of synthesizing foods out of air, water, and inorganic salts of the soil, so ordinarily they cannot remain anchored in one spot, manufacturing their foods out of raw materials at hand, but are obliged to forage for food already made.

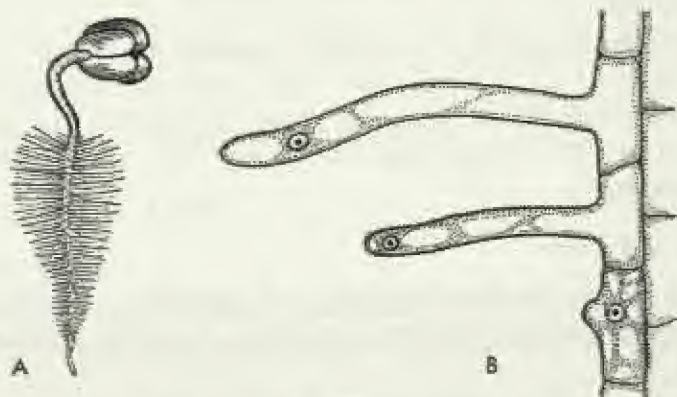


Fig. 209. Intake mechanism of plants. A, young seedling, showing root hairs; B, part of a section through a young root, showing some of the superficial cells growing into root hairs. A thin layer of cytoplasm (dotted) lines the cell wall and encloses the cell sap. (After Brown.)

Like plants, animals depend upon osmotic intake through thin cell membranes, cellular middlemen between indispensable food and the animal body, which cannot remain without harm on the outside of bodies of adventurous locomotor organisms. The intake cells of animals, as well as of plants, must be protected from mechanical injury and from drying up, while their possessors are seeking food. This explains the evolution in locomotor animals of the *digestive tube*, an enclosed passage-way arranged for one-way traffic and paved with thin-walled absorbing cells that correspond to the osmotic root hairs of plants. In one sense the digestive tube is simply an infolding of the integument, making a protected subway where food admitted at the entrance is exposed to intake cells, which proceed to do their osmotic duty in security without drying up while being transported to fresh fields of food supply. Thus, in a way, an animal may be regarded as a plant turned outside-in.

5. The Mission of the Food Tube

In the process of living, while energy is being released by the oxidation of the tissues, it becomes imperative that replacements be made from outside sources, or in other words, that food be obtained. It is not enough, however, simply to get food, since energy-containing substances cannot be utilized until they are so liquefied and transformed that they may be taken into the blood, to be forwarded to the needy tissues where the actual feeding, or incorporation of food materials, occurs. To accomplish these transformations is the mission of the digestive tube with its accompanying contributory devices.

The everyday miracle of a cat taking a captured mouse and changing it over into *more cat*, or of human flesh and blood, endowed with personal idiosyncrasies, made out of the hodge-podge of materials that appear on daily bills of fare, is so ordinary and familiar that these marvels have ceased to excite wonder.

6. Kinds of Feeders

Animals may be classified according to the prevailing character of their intake into herbivores, carnivores, omnivores, parasites, symbionts, and saprozoans.

Herbivores are direct plant feeders. *Carnivores* feed upon animals, but in reality are plant feeders at least once removed, since the ultimate food of all animals is plants. *Omnivores* feed directly upon both animals and plants. *Parasites* feed at the expense of living organisms which "entertain" them as "hosts" without necessarily fatal results. *Symbionts*, such as green hydras and certain green worms, live vicariously at the expense of microscopic green plants embedded in their bodies, which have the ability common to green plants of synthesizing food on the spot; while *saprozoa*, like certain flagellates and infusorians, are scavengers, specializing upon dead organisms in the last stages of their reduction into inorganic materials. Most vertebrates belong in the first three groups.

Animals with a wide range of foods have a better chance in the struggle for existence than those that have become specialized for a single source of nutrition, such as the pronuba moth, which feeds only on the pollen of the yucca flower; termites with a diet of woody cellulose; boll-weevils that spurn everything except cotton "squares" before they bloom; and coprophagous beetles that revel only in feces.

There are a few curious carnivorous plants, like the Venus fly-trap, bladderwort, pitcher plants, and sundews, that have deviated far from

the self-reliance of most green plants, which manufacture their own food. These isolated plants by various cunning devices have augmented the usual source of food of green plants by capturing small animals which they devour. A greater variety of plant forms, including bacteria and fungi that have no chlorophyll, live saprophytically on the dead organic remains of other plants.

Animals in satisfying their demands of hunger from all sorts of sources are quite unaware that the chemist finds only three fundamental kinds of food in the world, with certain necessary additional inorganic trimmings in the form of water and salts. These three basic food substances, which occur in an infinite number of guises in the bill of fare of animals and plants, are *proteins*, that furnish building materials for growth, maintenance, and reproduction, and *fats*, and *carbohydrates*, which supply the immediate energy indispensable to the business of living.

II. THE FOOD TUBE

1. Its Evolution

In the lowest unicellular forms of animal life, the osmotic process of taking in food substances is performed by the outside of the body, somewhat after the fashion of plants, as most simply demonstrated by *Amoeba*.

Among sponges, which take the first step in the great adventure of cell associations, the method of intake is hardly different, although there is a prophecy of an internal digestive tube in the ciliated passage-ways that honeycomb the loosely connected sponge mass, through which the food-laden water is made to stream.

Hydras, corals, and sea-anemones, as well as all other typical coelenterates, have a *digestive sac* open only at one end, and little else. This single external opening serves as both mouth and anus. In these pioneer animals everything is sacrificed to securing a suitable place for the bestowal of food. The very shape of the body is determined by the food sac, for the whole animal is simply an animated food bag, decorated around the intake opening with a fringe of subservient tentacles. The importance of the food cavity is thus clearly emphasized by its early establishment before most other structural refinements peculiar to the animal organism.

Even in echinoderms, although an anus is nominally present it plays only an occasional rôle, since these devastating, devouring creatures, of which starfishes and sea-urchins are typical examples, dispose so effectually of the food entering their maw, that there is very little waste left over for expulsion at the exit. As a matter of fact in the case of the starfish, most

of the food waste is not even taken into the mouth. Instead the stomach is everted from the mouth in feeding and enwraps the food or prey so completely that the indigestible parts are left behind when the stomach is withdrawn, leaving no residue to be passed out at the anus.

Worms and caterpillars may well be described as perambulating digestive tubes, with the important mouth end pointed toward a food-containing world. Directive sense organs cluster around this exploratory end of the food tube, informing it where to go.

A vertebrate in reality is a double tube. The outer tube is the protective body wall, and the inner tube, the digestive canal. Between the two tubes is the body cavity, which makes possible within a limited space the storage of a digestive canal much longer and more efficient than the exterior of the animal would lead one to suspect. Thus, the knapsack for carrying the rations is bestowed within the body instead of being carried outside.

2. Increase in Digestive Surface

So long as the bulk of an animal's body remains small a straight digestive tube has an adequate internal surface to meet all alimentary demands. It is mathematically demonstrable, however, that while the *surfaces* of two



Fig. 210. Comparison of the tadpole and the young frog, *Alytes*, just after metamorphosis, to show the great difference in the digestive tract with the change from plant to animal diet. (After Reuter.)

homologous solids are to each other as the *squares*, the *masses* are to each other as the *cubes* of their homologous dimensions. This means that the bulk of a growing animal increases more rapidly than its surface, with the inevitable result that a straight unmodified digestive tube becomes inadequate to take care of the accompanying mass. This is particularly true in the case of herbivores, whose food is less concentrated than that of carnivores, and who consequently need digestive machinery adequate for handling a larger quantity of food in a given time.

There are four general ways in which this need for increase of digestive surface has been met in various animals, namely, (a) by increase in diameter; (b) by increase in length; (c) by internal folds and elevations of various kinds; and (d) by the addition of supplementary diverticula.

(a) **Increase in Diameter.**—This method is not extensively employed, because of the limitations of space in the body cavity. If the inner tube

increases in diameter the outer tube of the body wall must also enlarge, which tends to defeat the object to be gained. Certain regions of nearly every digestive tube, such as the stomach and large intestine, are frequently, nevertheless, of greater diameter than the remainder of the tube.

(b) **Increase in Length.**—Increase in length is a universal device among vertebrates for adding to the available digestive surface, since the body cavity furnishes possible space for stowing away coils and loops of the tube. The body cavity not only makes a place for an intestine longer than the body itself, but it also frees the intestinal tube from the muscular control of surrounding tissues, permitting it freedom to exercise peristaltic movements of its own.

The characteristic swollen shape of a tadpole, resembling an animated head with a tail attached, is due to the enormously lengthened digestive tube which is coiled about many times, packing the body cavity full. Just

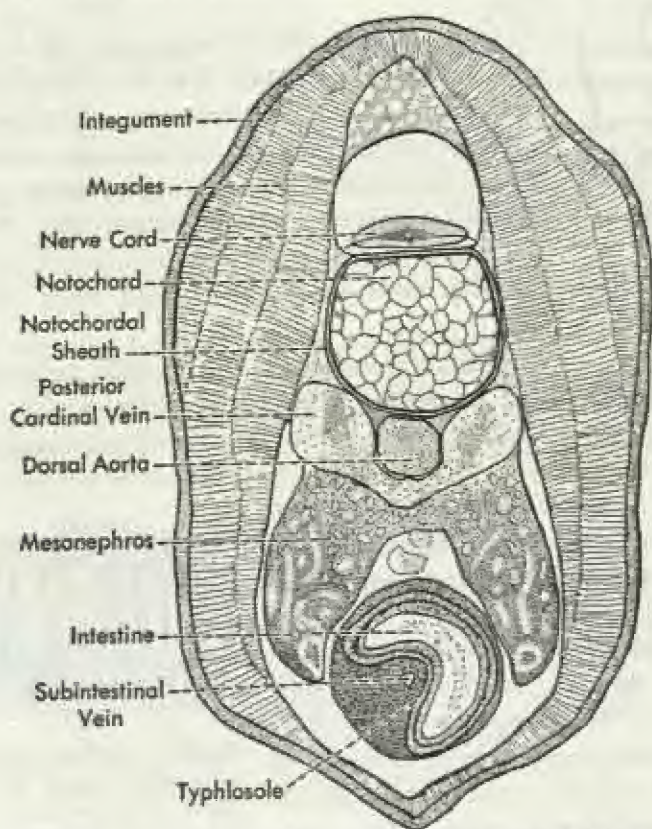


Fig. 211. Cross section through an ammocoetes larva of a lamprey eel, showing typhlosole which increases the internal surface of the digestive tract.

before metamorphosis, when the tadpole gut is adapted for plant food, it may measure eight to ten centimeters in length, whereas after metamorphosis, when the young frog switches over to insect food thus requiring less digestive surface, the tube shortens to three or four centimeters in length, although the body itself is now considerably longer than before (Fig. 210).

In man the entire digestive tube is between twenty-five and thirty feet in length, although the entrance and exit are only about two feet apart.

(c) **Internal Folds.**—Increases both in diameter and length of the digestive tube make demands that soon encroach upon limits of possible space within the body cavity. Internal folds within the food tube itself avoid this difficulty by adding to the expanse of surface to which the food is exposed without adding to the external size of the tube.

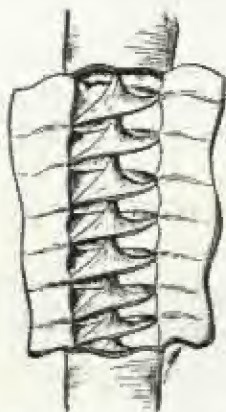


Fig. 212. Spiral valve of a dogfish. (After Roule.)

A longitudinal fold extending into the cavity of the tube is termed a *typhlosole* (Fig. 211). Such an arrangement is present in the cyclostomes. In dipnoans, as well as elasmobranchs and ganoid fishes, the intestinal part of the food tube is supplied with a *spiral valve* (Fig. 212), a typhlosole so much longer than the tube in which it is placed that it must coil around like a spiral stairway, with one edge attached while the other is free.

Certain invading transverse folds, called *plicae circulares* (Fig. 213), give a washboard effect to the inner surface of the anterior part of the human intestine, while countless tiny elevations, or *villi*, projecting like the nap of velvet from the inner surface of the small intestine, particularly in the higher vertebrates, produce, in a minimum of space, an enormous increase of absorbing area for contact with passing food.

(d) **Supplementary Diverticula.**—Side alleys, or diverticula, from the main tube occur in many instances. These are particularly abundant in fishes at the junction of the stomach with the small intestine, where they are called *pyloric caeca* (Fig. 214).

They vary in number from one in the ganoid *Polypterus* and the sand-lance *Ammodytes* to over 200 in the mackerel *Scomber*.

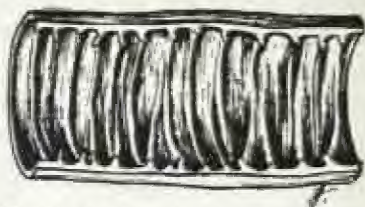


Fig. 213. Transverse rugae, *plicae circulares*, lining the intestine. (After Cunningham.)

Other diverticula, called *colic caeca*, are found at the junction of the small and large intestines in amniotes. The colic caecum of a turtle is only a slight enlargement (Fig. 215), but in rabbits and some rodents it may become an enormously enlarged tube with an internal capacity nearly equal to that of the rest of the digestive canal to which it is attached.

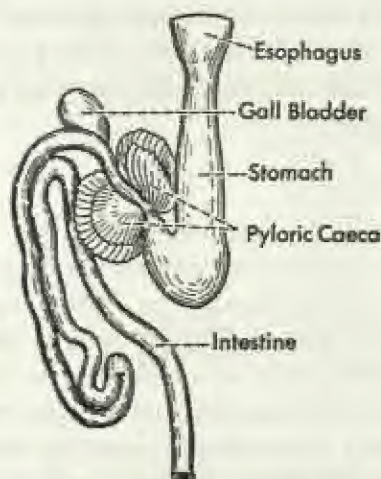


Fig. 214. Pyloric caeca of a teleost fish, *Merluccius*. (After Krupski and Schimkewitsch.)

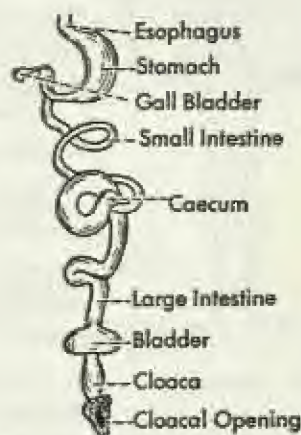


Fig. 215. Digestive tube of a turtle. (After Butschli.)

In man the colic caecum, with its troublesome shriveled prolongation, the *processus vermiformis*, or "vermiform appendix" (Fig. 216), has outlived its usefulness and bears an unsavory reputation. Birds have typically two colic caeca (Fig. 217).

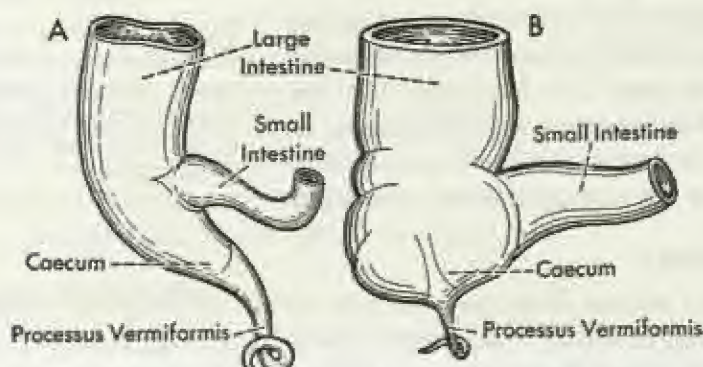


Fig. 216. Caecum and processus vermiformis (vermiform appendix) in man. A, in the embryo; B, in an adult. (After Wiedersheim.)

The large intestine of man, as well as of several other mammals, is pushed out into a series of baywindow-like enlargements (Fig. 218), which are diverticula of a sort called *haustra*. Connected with the rectal region throughout the vertebrate series are various problematical outpushings, such as the *rectal gland* of elasmobranchs; the *urinary bladder* of amphibians; the *bursa of Fabricius* in birds, and the *anal glands* of certain mammals, all of which have been made to serve different uses, although not necessarily connected with the process of digestion.

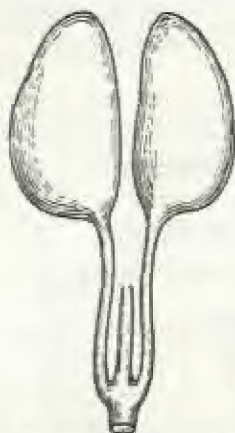


Fig. 217. Two colic caeca of an owl. (After Pycraft.)

3. Development

Mouth and anus are not essential during embryonic development when the body secures its nourishment either from the yolk mass or, in the case of mammals, from the maternal blood stream. There comes a time, however, when provision must be made to admit food into the digestive cavity from other sources. This necessity is met by the formation of two ectodermal invaginations, one near each end of the elongated archenteron, which break through to make a continuous open passage-way, the digestive tube (Fig. 117).

The anterior ectodermal ingrowth is called the *stomodaeum*, and the posterior ectodermal part, the *proctodaeum*, while the endodermal region between them, which was originally the archenteron, is now termed the *mesodaeum*. The embryonic stomodaeum stakes out the claim for the future mouth region; the proctodaeum locates the anus. The food tube thus consists of three embryonic components, although the landmarks that separate them from each other are obliterated in the adult.

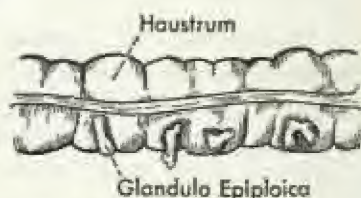


Fig. 218. Haustra of the large intestine of man, with small peritoneal pockets, *glandulae epiploicae*, attached to the outside of the intestinal wall. (After Cunningham.)

4. Histology

A cross section of the digestive tube within the body cavity shows it to be made up of several concentric layers of cells (Fig. 219).

The innermost layer, or *mucosa*, the original embryonic endoderm, is supported by mesodermal connective tissue, the *submucosa*. The *mucosa* is

only one cell-layer thick, except in the anterior esophageal region. It performs not only the "root hair" function of absorption, but also gives rise to various digestive glands whose secretions bring about chemical transformation of the food taken in. All the other layers aside from the mucosa are secondary and are subsequently added to this most important absorptive primary lining of the food tube.

The submucosa, next to the mucosa, is largely devoted to supporting a rich network of capillaries and lymphatics which bear away over the body the materials absorbed by the mucosa.

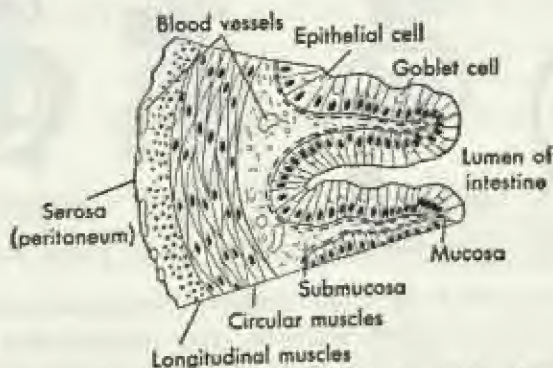


Fig. 219. Part of a cross section through a frog's intestine. (From Mavor, *General Biology*, copyright 1947, by permission of The Macmillan Company, publishers. After Holmes.)

Outside of the submucosa there is a double layer, the *muscularis*, composed of circular muscles on the inside and longitudinal muscles on the outside. These muscles are involuntary in their action, except for a short distance at either end of the tube in the stomodaeal and proctodaeal regions, where they are under the control of the will. They effect movement of the food through alternate contractions by processes of *segmentation* and *peristalsis*. Segmentation churns the contents of the tube back and forth, while peristalsis forwards it.

Protecting the muscular layers on the outside is a sustentative layer of tissue called the *serosa*, which is continuous with the mesenteries and with the peritoneum that lines the body cavity. In that part of the tube lying outside of the abdominal cavity, no serosa is present.

5. Regions of the Tube

Since food undergoes progressive modification as it passes through the digestive tube, the tube itself, as would be expected, shows structural adaptations for the performance of these various tasks. Of necessity there has

evolved a physiological division of labor, or specialization, which has left its mark on the morphological features that characterize the alimentary tract in different regions. For purposes of description the entire tube may be divided into four zones, or regions, namely, ingressive, progressive, degressive, and egressive.



Fig. 220. Silhouettes of the digestive system. (After Roule.)

The *ingressive zone* is the intake region of prehension and mastication. It involves the lips and mouth with the teeth, tongue, and various other structures contained therein. The *progressive zone*, embracing the pharynx, esophagus, and stomach, is the region of forwarding the food-intake and passing it through the preliminary stages of modification. The *degressive zone*, coincident with the small intestine, is not only the most extensive but also in a sense the most important part of all the zones, for here occurs the chemical preparation of the food stuffs, and their ultimate selection and absorption into the blood. Finally, the *egressive zone*, which is confined to the large intestine, is the region for the expulsion of the unusable residue that cannot be diverted into the blood and applied to the uses of the body. These regions are shown diagrammatically in silhouette for fishes, amphibians, birds and mammals, in Figure 220. With this introduction we may now proceed upon an imaginary tour of inspection through the entire alimentary tract, with our eyes open for the anatomical scenery along the way.

III. INGRESSIVE ZONE

1. Food Capture and Prehension

Before food can travel along the digestive highway, it must be captured and placed inside the entrance of the tube. This process, which may call for expert performance, occupies a large part of the waking hours of most

animals, and even in the case of intellectual man is the actuating motive behind much of his daily behavior. It is no concern of plants.

Probably in the majority of cases the capture of food involves some sort of a chase, since the animal as well as its food may be in motion. Herbivores have the advantage of depending upon food that is generally stationary, so they simply need to seek it out. Sedentary feeders, on the other hand, remain in one spot, catching motile food that comes their way. Devices of various kinds, therefore, like ciliary whirlpools or stretching tentacles, are employed by stationary animals to bring food within range. Many aquatic animals that are not sessile also use cilia to sweep microscopic food particles their way. The ciliated fraternity includes protozoans, sponges, anthozoans, bryozoans, rotifers, brachiopods, sessile annelids, brittle-stars, bivalves, pteropods, entomostracans, tunicates, amphioxus, and many larval forms.

Many animals that are anatomically able to go in pursuit of food, succeed better by lying in wait for passing food than by bestirring themselves in open chase. They have their breakfast, so to speak, served to them in bed. Such animals frequently develop camouflaging coloration, or, like spiders, construct elaborate snares and traps for their prey. Mucous threads are employed by certain coelenterates and mollusks to entangle food particles that are then engulfed. With the evolution of bilateral symmetry and increased powers of locomotion, "watchful waiting" goes more and more into the discard and pursuit of daily bread becomes the more universal method.

When food is finally within reaching distance, there are many diverse organs of prehension (Fig. 221), which come into play for seizing it and placing it within the mouth. These adaptations range all the way from the slow pseudopod of an *Amoeba* to the reaching "boarding house arm" of modern man.

Birds, possessing neither arms nor hands for taking hold of food, have the edge of the mouth opening drawn out into a point, forming a horny beak which is used as a pair of forceps in picking up things.

The prehensile tongue of such diverse animals as toads, anteaters, and

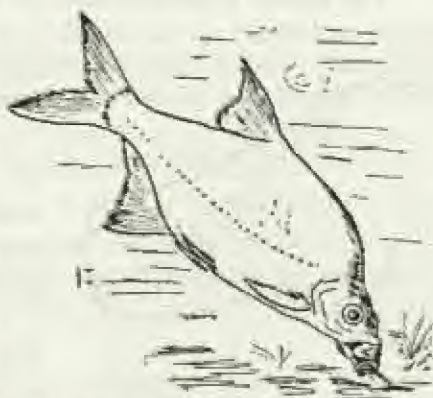


Fig. 221. A fish with a protrusible mouth, pulling an insect larva out of the muddy bottom. (After Hesse.)

cattle, becomes a very effective substitute for a grasping hand, while muscular lips, particularly of herbivores, serve a similar purpose in food prehension.

Some snakes, with no means for killing their prey when it is overtaken, seize it with their backward-projecting teeth and swallow it alive. When once within the mouth it cannot easily be ejected or escape, but is forced to inch its way down the gullet by the propalinal motion of the jaws.

Many animals, as for example swans and giraffes, have an elongated flexible neck as an accessory organ of prehension, to aid in bringing the mouth into the immediate neighborhood of food. The trunk of an elephant, which is a drawn-out nose and upper lip combined, is a unique device for reaching food without the necessity of lowering the heavy head.

Certain annelids and starfishes prehend their food by everting the pharynx, or the stomach, as the case may be, which enwraps the food and may even digest it outside the body.

2. The Mouth Aperture and Lips

The mouth is the architectural centerpiece of the face (Fig. 222). The shape and extent of the mouth opening varies greatly in different animals, depending largely upon the different kinds of food utilized.



Fig. 222. Head of a hippopotamus, showing the projecting face. (After Hitzheimer.)

The limits of the oral slit in mammals are set by the fleshy cheeks. An animal without cheeks, like an alligator or a nestling bird, can open up the mouth to a surprising extent.

Amphioxus and cyclostomes (Fig. 145) keep the mouth always open of necessity, since structurally it cannot be closed. In man the slit of the mouth normally extends from about the region of the first premolar teeth on one side to those on the other side, although there is considerable range of individual variation, as may be commonly observed.

The puffed cheeks and rosebud mouth of infancy are muscular adaptations for sucking, mammalian characteristics which are largely lost in adult life (Fig. 223). The evolution of cheeks in the adult is closely connected with the muscular equipment for mastication, so it comes about that animals with relatively small mouth openings are usually better able to chew their food than those with an expansive opening. Cheeks and chewing go together, for cheeks make possible the retention of food between the grind-

ers. The retaining cheeks of cattle enable them even to chew "up hill" (Fig. 224). The refinement of chewing food, with all its train of anatomical consequences, is a mammalian peculiarity, for it will be recalled that fishes, amphibians, birds, reptiles, and even many of the lower mammals, swallow their food without chewing it.



Fig. 223. The profile of infancy. (After Bell.)



Fig. 224. The mastication plane of a cow which makes it necessary to chew "up hill."

In the higher vertebrates the lips are two movable folds at the edge of the mouth aperture. They are covered by skin on the outside and moist mucous membrane on the inside. The red part of a lip, an exposed zone of transition between skin and mucous membrane in man, is extremely sensitive to touch because of an abundant supply of nerve endings. The lower lip is more movable than the upper one. Attention to the form and shape of these portals to the digestive tube is shared alike by the comparative anatomist and the poet.

3. Buccal Cavity

Immediately within the mouth aperture of mammals is the vestibule, or *buccal cavity*, bounded outwardly by the lips and cheeks, and inwardly by the external face of the teeth and gums. When the mouth is closed and the teeth are in contact, this cavity becomes practically obliterated, but behind the back teeth, and between the closed teeth, there is still direct communication with the larger *oral cavity* within.

Various glands open inside the buccal cavity. Along the inner surface of the lips are numerous small *labial glands* that secrete mucus. These glands may be easily identified by rubbing the point of the tongue back and forth against the inner surface of the lips, when they will be felt as tiny bunches. Other mucus-producing glands, the *molar glands*, open from the cheeks

into the buccal cavity opposite the back teeth, while opposite the second upper molar tooth on either side, is the exit of *Stenson's duct* that drains the large *parotid gland* (Fig. 225), from which saliva flows. It is not difficult to locate the openings of these important ducts, for if one sticks the tongue into the cheek, and psychologically aids the flow of saliva by looking at a freshly sliced lemon, or something that "makes the mouth water," a tiny stream of saliva may be felt spurting into the buccal cavity.



Fig. 225. Salivary glands and their ducts. (After Cunningham.)

Birds, turtles, and monotremes with beaks, have dry cornified buccal cavities nearly devoid of glands. No one ever saw a bird "spit."

Saliva, containing a digestive enzyme, *ptyalin*, is produced at the rate of as much as three pints a day, for the most part during the intake of food. Since saliva is not stored, the glands need periods of rest and recuperation between times of accelerated activity. The reader can draw his own conclusions about the physiological results of the gum-chewing habit.

On the inner face of the upper lip in the middle line, demonstrable by the exploring tip of the tongue, is a vertical fold of mucous membrane which tends to hold the lip close against the gums. This is called a *labial frenulum*. A second one occupies a similar median position with reference to the lower lip.

In some animals, such as the duckbill, Old World monkeys, apes (Fig. 226), gophers, squirrels, and other rodents, the buccal cavity can be stretched into distinct *cheek pouches*, which are used for the temporary storage of

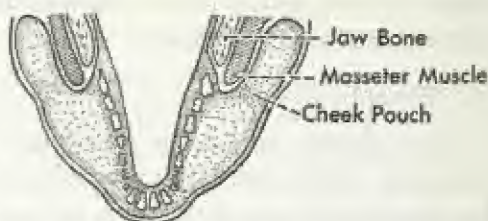


Fig. 226. Lower jaw of ape, showing lateral cheek pouches. (After Nuhn.)

food when its collection occurs under circumstances of competition such as to make grabbing as much as possible in a minimum of time desirable. Sometimes greedy little children demonstrate their probable rise from animal ancestry by reverting to the cheek-pouch method of excess disposal of food.

4. Oral Cavity

Behind the mammalian buccal cavity and merging into it, is the *oral cavity*. The *roof* of this cavity, in higher vertebrates generally, is the arching palate which has a skeletal foundation of bone, the *hard palate*, in the front part of it, and is supplemented behind by a flexible addition of connective tissue, the *soft palate*.

The hard palate lies within the upper dental arch and is continuous with the *gums* (*gingivae*), that are rich in blood vessels but poor in nerves. The soft palate blending with the lateral walls behind the teeth, presents a free posterior border hanging like a curtain, in the region of the *fauces*, or the gateway leading to the pharynx.

The posterior border of the soft palate in man is still further prolonged in the median line into a soft, pointed, dangling flap called the *uvula*, that projects downward and backward, and which may easily be seen hanging down in the back part of a wide-open mouth (Fig. 227).

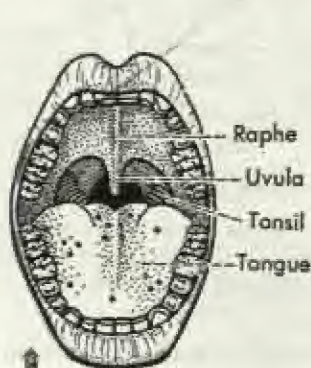


Fig. 227. Open mouth showing uvula, tonsils, and median raphe. (After Cunningham.)

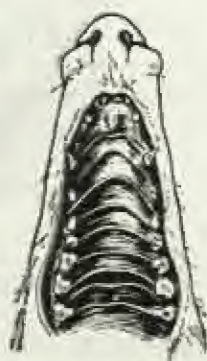


Fig. 228. Palatine ridges in the roof of a dog's mouth. (After Wiedersehlm.)

Along the median line of the human hard palate, from a point near the upper median incisor teeth and fading out toward the region of the soft palate, is a faint ridge, the *raphe*, which indicates that the hard palate is formed by the union of two lateral components. It may be felt, in those individuals who still have it present in the roof of the mouth, by means of the tip of the tongue.

In many instances there may also be similarly demonstrated a series of transverse folds or ridges at right angles to the raphe, the *palatine rugae*,

diminishing in size from the region of the teeth backward. The rugae are more in evidence in human embryos than in adults, although they not infrequently persist throughout life. They are wash-board like in character and find their highest development in such carnivores as cats and dogs (Fig. 228), where no doubt they aid in securing a surer grip upon any struggling victim that has been seized in the jaws.

The surface of the entire palate, particularly of the soft palate and the uvula, is beset with numerous *palatine glands*, whose secretion of mucus helps to keep the mouth cavity moist.

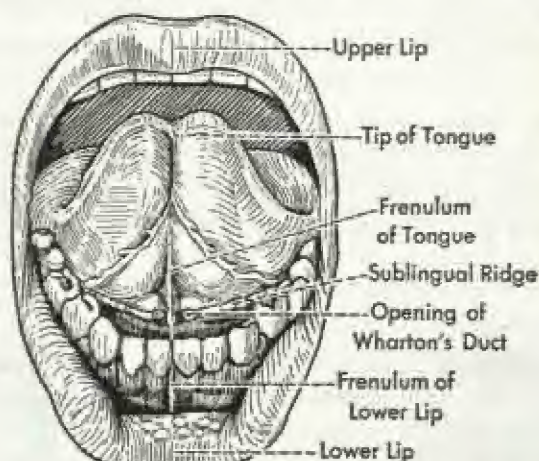


Fig. 229. The mouth, widely opened, with the tip of the tongue drawn upwards, to show the frenula of the tongue and lower lip, the openings of Wharton's ducts, and the sublingual ridges. (After Toldt.)

The *sides* of the oral cavity posterior to the back teeth blend with the buccal cavity into a common space, while the *floor* is largely occupied by the bulky tongue, which fills practically the entire cavity when the mouth is closed. When the mouth is opened wide and the tongue is raised and curled back, the *frenulum linguae* may be seen in the shape of a fold of connective tissue along the midventral region, that tends to hold the tongue down to the floor of the oral cavity (Fig. 229). Occasionally, when the lingual frenulum is overdeveloped in a human infant, such an individual is said to be "tongue-tied," and a slight surgical operation is necessary before the tongue can acquire the freedom of movement essential for clear articulation in speech.

Extending on either side of the frenulum linguae in man, and parallel to the lower teeth, is a crescentic fold of tissue, called the *sublingual ridge*. Along this ridge open the several ducts of Rivinus from the sublingual sali-

vary glands, while at the widest part of the frenulum linguae, near the lower median incisor teeth on either side, are the openings of *Wharton's ducts*, that drain the *submaxillary salivary glands*. Thus, three sets of salivary glands, the parotid, sublingual, and submaxillary, pour their digestive and lubricating secretions of saliva into the buccal and oral cavities.

This differentiation of mouth glands into various mucous and salivary glands common to mammals does not appear among the lower vertebrates. Fishes, which bolt their food without chewing, do not have digestive salivary glands, while mucous glands, the mission of which is to moisten the food in the oral cavity preparatory to swallowing it, are also unnecessary and practically absent.

Among amphibians, living on the border line between submergence in water and life on land, scattered mucous glands, termed *intermaxillary glands* from their generalized location, make their appearance in some instances, while the protrusible tongue, particularly in frogs and toads, is supplied with *lingual glands*, secreting a viscous mucus that aids in the capture of insects and other moving prey.

In reptiles the mouth glands are more grouped and localized, so that it is possible to speak of *palatine*, *lingual*, *sublingual*, and *labial glands*, according to their location. All of these glands produce fluid that moistens the food and renders the act of swallowing easier, although it is doubtful if they aid appreciably in digestion.

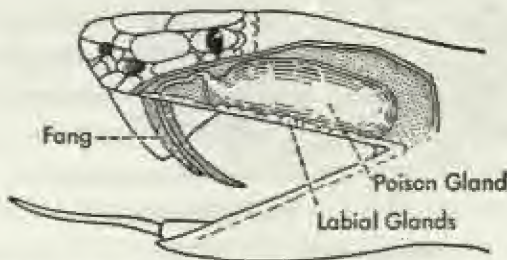


Fig. 230. Poison gland of a rattlesnake, with duct passing into fang.
(After Kingsley.)

Poison glands in the mouth of certain snakes (Fig. 230), are transformed parotid glands, while those of the only lizard known to be poisonous, the "gila monster," *Heloderma*, of the southwestern United States, are modified sublingual glands.

Birds, as noted, have a paucity of oral glands.

In the case of mammals, which usually chew their food to some extent, mouth glands of two general sorts are universally developed, mucous and

salivary, for the double purpose of lubrication, and of liquefaction and chemical modification. Mucous glands are especially essential for herbivores that consume large quantities of comparatively dry, bulky food. The action of the salivary glands, which is both chemical and mechanical, will be referred to later in the consideration of digestive glands in general (see Fig. 271).

5. Tongue

What passes under the name of "tongue" in the vertebrate series is not always strictly comparable to the "unruly member" in man (or woman), which must be regarded as the outcome of a long sequence of adaptations.

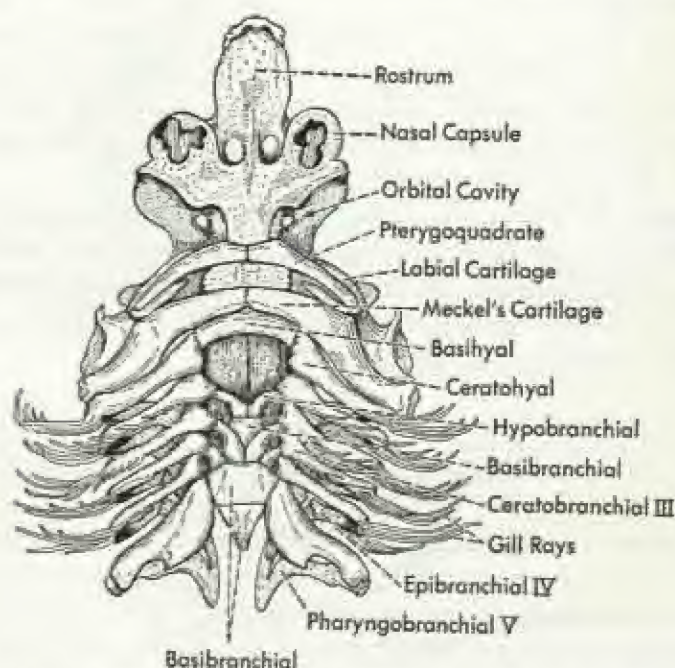


Fig. 231. Diagrammatic ventral view of the splanchnocranium and neurocranium of *Squalus acanthias*. The basihyal cartilage, lying between the two sides of the lower jaw, is the skeletal basis of the fish's tongue.

Amphioxus has no tongue at all, and the muscular piston-like tongue of cyclostomes is such an aberrant, highly specialized structure that it gives no safe clue to the true beginnings of this organ among vertebrates.

In fishes, however, a *primary tongue* makes its definite appearance. It is a non-muscular elevation from the floor of the mouth cavity, consisting of a covering of mucous membrane, stretched over a skeletal support of

cartilage or bone, derived from the framework of the gills (Fig. 231). A projecting *basihyal cartilage*, that lies between the lower jaws of the mandibular arch, is the skeletal basis of this kind of a tongue. Whatever movement it is capable of is due to extrinsic muscles that act upon the skeletal support in such a way as to enable it to change position but not shape, rather than upon intrinsic muscles that modify both shape and position. It is also not protrusible, although motile enough to aid somewhat in forcing back a mouthful of food to be swallowed, and, in some cases, is beset with prehensile teeth.

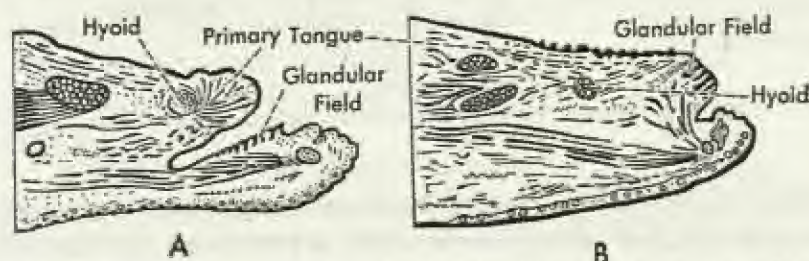


Fig. 232. Median section through the floor of the mouth, showing the formation of the glandular tongue. a, *Triton alpestris*; a, *Salamandra maculosa*. In the latter the glandular field is encroaching upon the primary tongue to form the secondary tongue. (After Haller.)

The lower amphibians, such as the perennibranchiate urodeles, have fishlike tongues of mucous membrane with cartilaginous support. In the higher salamanders the horseshoe-shaped groove between the primitive tongue and the lower jaw becomes elevated, particularly in front, into a *glandular field* (Fig. 232), in which a glutinous mucus, useful in entangling captured insects, is secreted. This glandular field gradually rises, thus obliterating the original groove around the under edge of the primary tongue, until finally it becomes incorporated with the latter as an anterior projection, forming the so-called *secondary tongue*.

In the median line at the junction of the primary and secondary tongues, and originally connected with the thyroid gland, there is a tubular down-growth, the *thyroglossal duct* that persists in mammals as the *foramen caecum* (Fig. 233).

The secondary tongue soon becomes invaded by intrinsic muscles, which greatly increase the range of its movements, and make changes in its shape possible. Of these muscles the *genioglossals* act as protractors, and the *hyoglossals*, as retractors. In the American salamander *Eurycea*, they become so efficient that the sticky tongue may be shot out a considerable distance and retrieved with incredible speed in the capture of insect prey.

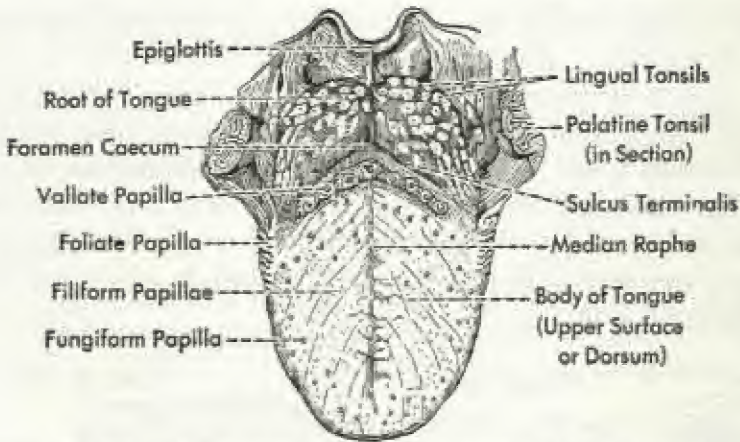


Fig. 233. Dorsal view of the human tongue. (After Toldt.)

The secondary tongue of most frogs and toads, which is attached far forward on the floor of the mouth cavity, is retroflexed when at rest, so that its point lies backward down the throat. When it is flipped out after an insect (Fig. 234) or a slug, it is "swallowed" upon its return, along with the captured food, and thus restored to its original position. One family of



Fig. 234. Tongue of a toad catching a fly.

toads, including the genera *Pipa* and *Xenopus*, is named Aglossidae, because in these exceptional animals, the tongue is either absent or very poorly developed.

Reptiles embryonically possess a double tongue, like that evolved by amphibians, although with considerable modification. In turtles and alligators it is thick and only slightly protrusible, whereas in snakes and lizards it may become extremely extensible. The little wall lizards, or "geckos," for example,

can easily lick the outside of their transparent eyelids with their tongues, while snakes can protrude their delicate sensitive forked tongues for some distance through a median notch in the edge of the lower jaw, without opening the mouth.

The chameleon (Fig. 41), an arboreal African lizard famous for its kaleidoscopic color changes, while grasping the twig of a tree uses its long tongue like a lasso in entangling its elusive prey, in much the same way as the salamander *Eurycea* from a position on the ground shoots out its

tongue. The mechanism in the two cases is somewhat different. In *Chameleon* the bony framework of the primary tongue acts as a system of extensible levers to supplement the secondary muscular component of the tongue in its protrusion, which is not the case with *Eurycea*.

In birds the bony framework of the primary tongue, which supports the secondary tongue, is especially well developed. This framework consists typically of a median bone or bones, the *copula* (Fig. 235), and two pairs of lateral bones, the small *hyoids*, and the *first branchials*, all of which are relics of ancestral gill arches. Its movement is facilitated by means of extrinsic muscles attached to these bones, the intrinsic muscles of the secondary tongue being reduced or absent.

A woodpecker, whose horny spearlike tongue can be projected out of the long beak when impaling a grub in the bark of a tree, possesses an elaborate skeletal hyoid apparatus attached at the base of the tongue, and with long posterior horns (first branchials) lying just beneath the skin. When at rest each of these horns extends from the tongue into the neck, then dorsally and forward over the top of the skull, reaching even into the base of the beak (Fig. 236). As the tongue is extended the springy supporting hyoid coils are straightened out through the action of muscles, while the withdrawal of the tongue to its original position within the beak is accomplished by the elasticity of the hyoids which snap back into place like released watch-springs that have been temporarily straightened out.

The mammalian tongue, like that of reptiles, is made up of two parts. The anterior region, somewhat rough and covered with numerous small elevations (*papillae*) of various shapes, is separated from the posterior part, bumpy in appearance due to masses of lymphoid tissue (*lingual tonsils*), by a V-shaped groove, the *sulcus terminalis* (Fig. 233). In the mid-line, at the posteriorly directed apex of the sulcus, is a small invagination, the *foramen caecum*, the remains of the *thyroglossal duct* by which the embryonic thyroid gland communicated with the oral cavity.

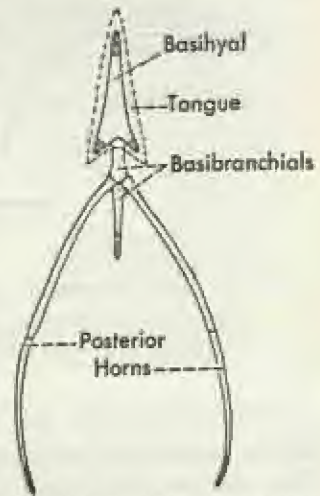


Fig. 235. Tongue apparatus of a pigeon. Basihyal corresponds to primary tongue. To the branchial arch elements (basibranchials and posterior horns of hyoid apparatus) are attached the extrinsic muscles of the tongue. Cartilaginous parts are stippled. (After Parker and Haswell.)

The papillae on the anterior section of the tongue, usually associated with taste buds, are of four types, namely, filiform, fungiform, foliate, and vallate.

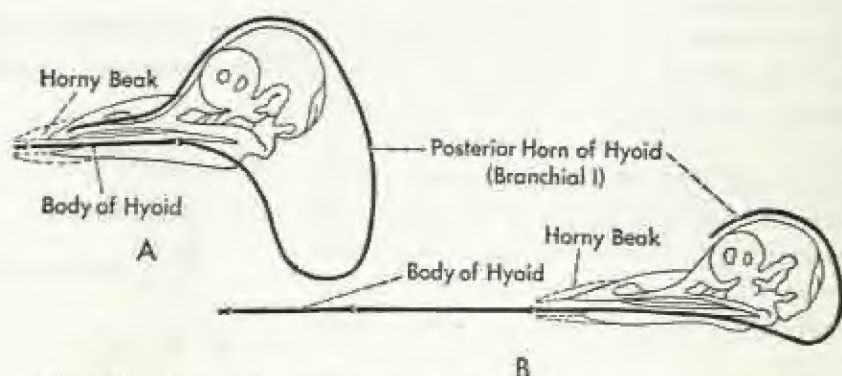


Fig. 236. Schematic representation of the position of the hyoid apparatus in the woodpecker. A, with the tongue withdrawn; B, with the tongue extended. (After Leiber.)

Filiform papillae are tiny threadlike or conical projections that are largely responsible for the velvety appearance of the surface of the tongue. They are not particularly associated with taste buds, although they serve to retain food solutions temporarily. In many mammals the filiform papillae become capped over with corneal material, taking on a mechanical rasp-like character, as shown by the tongues of cats and cattle, who use this device not only in eating but also as a hair brush.

Fungiform papillae (Fig. 237) are elevations from the surface of the mucous membrane that suggest the shape of a mushroom, hence their name. They are beset with taste buds and serve to bring these chemical receptors into contact with food solutions in the mouth cavity. Over the surface of the human tongue there may be as many as three or four hundred of these papillae, but they are always better developed in children than in adults. They are more numerous along the sides of the tongue than elsewhere, and have the appearance of small red spots.

The *foliate papillae*, which are usually located near the base of the tongue, are tiny ridges bearing taste buds. In man there are only three to eight of these ridges, but in rodents their number and size is greater.

The most elaborated of all the modifications for the display of taste buds are the *vallate papillae*. These resemble projecting knobs, surrounded by deep grooves, like the moat around a mediaeval castle, that serve to retain dissolved food substances. In the human fetus taste buds are distrib-

uted even over the tops of the knobs, but in adults they are confined to the sunken walls of the moats, where they are not only in direct contact with solutions to be tested, but are also protected from mechanical injury to which they would be liable at the surface.

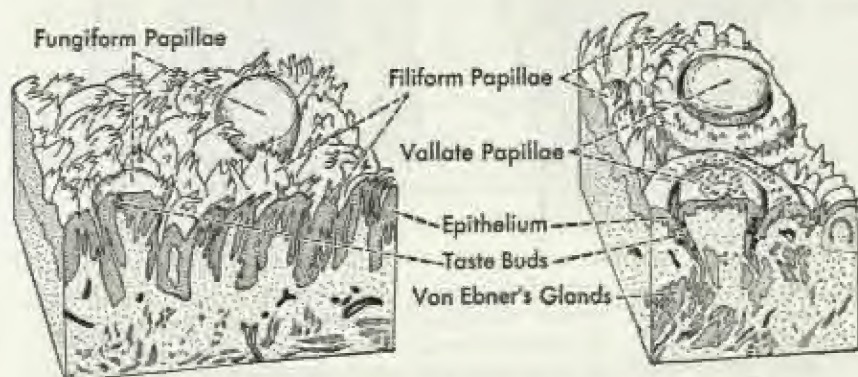


Fig. 237. Portions of the tongue of man showing lingual papillae in surface view and in section. Anterior toward the left in each drawing. (After Braus.)

Serous glands, called *Von Ebner's glands*, open at the bottom of the moats and aid in keeping them filled with fluid.

Vallate papillae are usually arranged in rows at the back of the tongue. There are two rows in monotremes, moles, bats, hares, pigs, horses, and edentates; three rows in marsupials, squirrels, many insectivores, and apes; four rows in the monkeys, *Macacus* and *Cercopithecus*; and a single row, arranged in a V-shaped formation in front of the sulcus, in the dog and man. They are missing in guinea pigs and coneys.

The posterior part of the tongue is derived from the bases of the hyoid and first two branchial arches, while the anterior or secondary tongue arises embryonically from a median and a pair of lateral swellings. In the human embryo of about four weeks of age, the secondary tongue first appears as an elevation from the floor of the mouth cavity just anterior to the landmark of the ductus thyroglossus. This elevation, which is homologous with the "glandular field" of the amphibians, is called the *tuberculum impar* (Fig. 238). On either side of it are *lateral lingual swellings* from the inner surfaces of the two sides of the skeletal mandibular arch, which meet at this point. These swellings soon increase until they completely surround the tuberculum impar, eventually forming the bulk of the anterior part of the tongue. In somewhat similar fashion the *copula*, the region enveloping the basihyal skeletal part that forms the foundation of the primary tongue lying

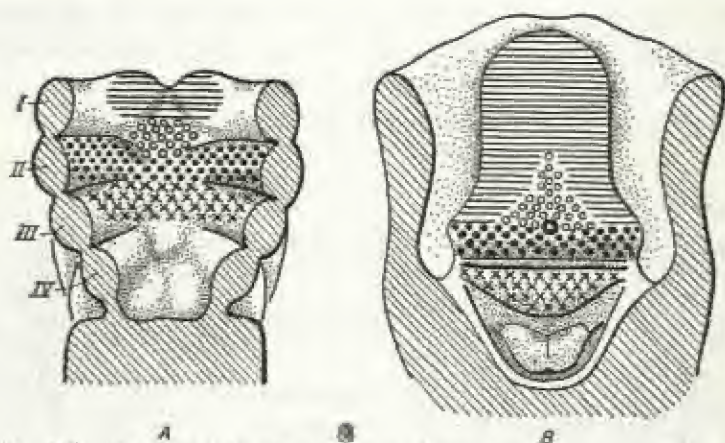


Fig. 238. Stages in the development of the human tongue. A, 6 mm embryo; B, 15 mm embryo. Contributions from the first three branchial arches (I, II, III) are indicated respectively by horizontal parallel lines, dots, and crosses; the *tuberculum impar* is marked by circles. (After Arey.)

behind the thyroglossal duct, is augmented by additions from the neighboring hyoid and anterior branchial arches, to form the "root" of the tongue, the part lying in the pharyngeal cavity (Fig. 239).

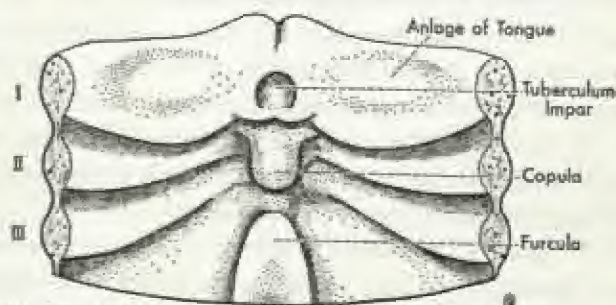


Fig. 239. Floor of the mouth and pharynx of a 7.5 mm human embryo, from a reconstruction. The swellings on either side, indicated by the halo of dots on the first branchial arch, give rise to the body of the tongue. (After McMurrich.)

The tongue of mammals serves many purposes and in consequence of the detachment of its anterior portion from skeletal elements is capable of great freedom of movement. It keeps the food between the teeth during the process of chewing, and starts it on its way when it is ready to be swallowed. It is also decidedly prehensile in many herbivores as already mentioned. Cows, for example, can grasp a tuft of grass with the tongue, to be sickled off against the lower incisors. It is a universal toothbrush giving

point to the phrase "as clean as a hound's tooth," and it also serves as a currycomb for fur-bearers, while animals like cats and dogs that lap up liquids use it as a spoon. Finally, its dorsal surface is thickly beset with sense organs of touch and taste, which stand in readiness to receive the password of admittance from entering food. In the human female it measures about three and a half inches in length—when at rest.

6. Teeth

Teeth are primarily devoted to the manipulation of food within the mouth cavity, to purposes of grasping, cutting or grinding, although in some instances they secondarily assume other functions, such as prehension of food, defence, offence, or even as aids in locomotion, as in the case of the walrus which uses its tusks in dragging its slippery body out of arctic water on to ice (Fig. 60).

The extreme diversity of teeth, adapted to their many uses, affords the comparative anatomist much insight into the manner of life of different animals, while to the palaeontologist they are preserved tokens which, like hieroglyphics, aid in reconstructing the story of the long-vanished past.

Teeth are the first hard structures of the body to put in an appearance during vertebrate development, even before any part of the bony skeleton. Although they eventually come into intimate secondary relation with the skeleton, they are in reality derivatives of the stomodaeal region of the alimentary tract. Thus these integumentary derivatives, homologous with placoid scales, become morphologically, as well as physiologically, a part of the digestive system.

(a) **Structure.**—In structure a typical mammalian tooth (Fig. 240) consists of a *crown* which projects beyond the gums; *roots* that are embedded in a socket of the jaw; and the *neck*, which is the transitional region between the crown and roots. Inside the hollow tooth is the *pulp cavity*, harboring blood vessels and nerves that gain access through a passage-way usually remaining open at the base. So long as this opening is unobstructed the tooth can continue to grow,

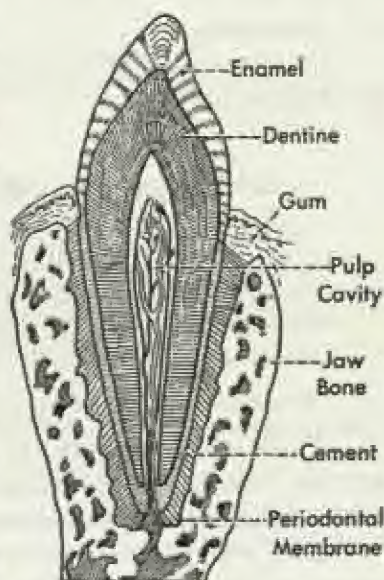


Fig. 240. Diagrammatic long section through a typical canine tooth.

as gnawing teeth of rodents do, by means of inside additions of tooth material. In most of the teeth of higher vertebrates, however, the opening of the pulp cavity becomes so constricted that after a certain size is attained growth ceases and, as the tooth wears away by attrition on the outside, there is no restoration.

The solid part of the tooth is three-fold in character. The bulk of it is *dentine*, or "ivory," a tissue denser than bone but, like it, permeated by tiny radiating canals, due to the fact that the dentine material is secreted around the branches of embryonic cells, the *odontoblasts*.

Over the crown, wherever exposed to wear, the dentine is usually protected by a layer of *enamel*, likewise penetrated by very minute canals in the lower forms but solid and prismatic in structure in higher vertebrates. Although not cellular in itself, enamel is the product of cellular activity and is the hardest, densest, most enduring part of the vertebrate body.

Outside of the dentine around the roots of the tooth, in those cases where the tooth is set in a socket, there is a bonelike substance, *cement*, that anchors the tooth firmly to the jaw. In ungulates the cement extends over the crown.

The composition of the dentine and enamel in the human tooth is given by Owen as follows:

	DENTINE	ENAMEL
Calcium phosphate and fluoride . . .	66.72	89.82
Calcium carbonate	3.36	4.37
Magnesium phosphate	1.08	1.34
Other salts83	.88
Organic matter	28.01	3.59
	<hr/> 100.00	<hr/> 100.00

(b) **Development.**—In the development of teeth six steps may be recognized, namely, dental lamina, enamel organ, dental papilla, crown formation, root formation, eruption.

About the seventh week in the development of the human embryo, certain Malpighian cells of the epidermis along the edge of the jaws, where the future teeth are to be, start into accelerated activity, pushing down into the underlying dermal tissue in the form of the so-called *dental lamina* (Fig. 241). Along this lamina at intervals wherever a tooth is destined later to appear, groups of these Malpighian cells proliferate into spherical *enamel organs*, which later lose their connection with the dental lamina. Under each enamel organ a tubercle of mesenchymal cells constituting a

dental papilla is formed, and presses the enamel organ into the form of a double-walled cup.

Crown formation follows through the interaction of cells of both papilla and enamel organ. The cells of the dental papilla are *odontoblasts* which secrete the dentine on their outer surfaces, thus producing the bulk of the tooth. The cells of the enamel organ next to the odontoblasts are *ameloblasts* which secrete a cap of enamel on the dentine. Meanwhile, capillaries and nerve endings invade the dental papilla and occupy the beginning of the *pulp cavity*.

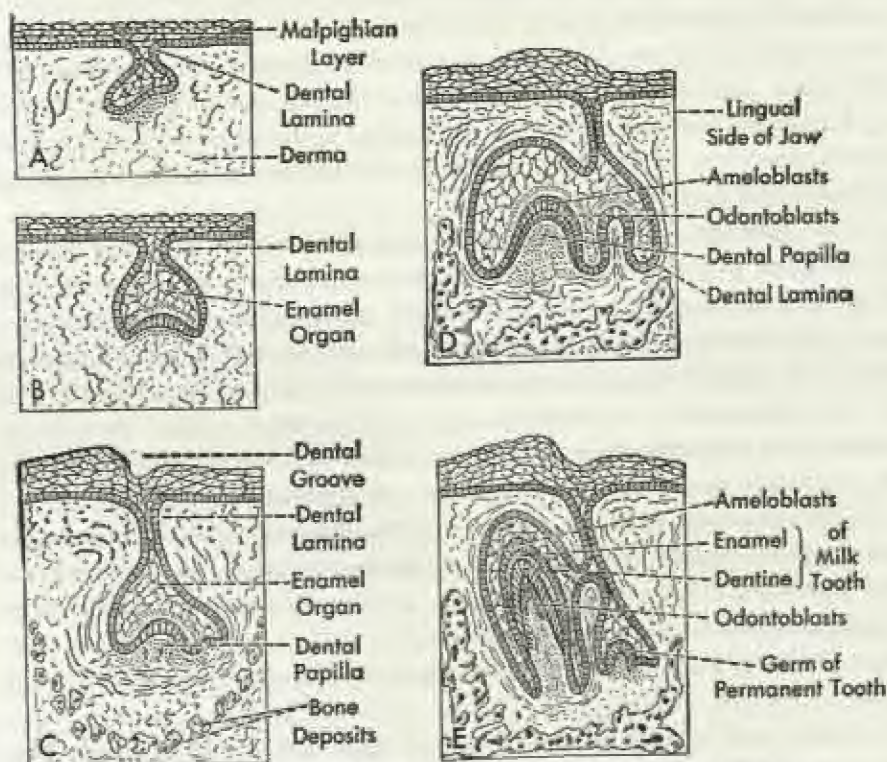


Fig. 241. Development of teeth. A, dental lamina stage; B, enamel organ stage; C, D, early and later dental papilla stage; E, crown formation. (A-C, after Maximow and Bloom; D and E, after Parker and Haswell.)

Root formation occurs sometime later, beginning just prior to the eruption of the tooth. The cells of the edge of the invaginated cup have continued to extend deeper into the tissue of the jaw but these deepest cells do not secrete enamel. Consequently the root, formed entirely by odontoblasts, is composed solely of dentine. As the root elongates it pushes the

completed crown through the enamel organ and more superficial tissues until the crown emerges and becomes almost entirely exposed. This process of eruption is known as "cutting the teeth." Around the dentine of the embedded roots of each tooth is deposited, through the activity of neighboring mesenchymal cells from the derma, the *cement tissue*, which aids in fixing the tooth in the jaw.

Permanent teeth of man are formed in much the same manner as described above for the milk teeth. The enamel organ arises, however, from the original dental lamina, on the lingual side of the first tooth germ in the case of teeth which are to fill in places vacated by "first teeth."

Like the placoid scales of elasmobranch fishes with which they are homologous, teeth are compound structures of diverse origin, arising from ectodermal ameloblasts, mesodermal odontoblasts, and mesenchymal cells.

The horny, rasplike "teeth" of the jawless cyclostomes are entirely ectodermal structures composed of cornified cells and not homologous with the teeth of other vertebrates.

(c) **Number.**—Lower vertebrates generally have an indefinite number of teeth, but in mammals the number becomes definite and limited. A reduction in the number of teeth is a mark of evolutionary advance associated with terrestrial life, less food, more chewing, shorter jaws, and stronger muscles of mastication, whereas an increase in the number of teeth, such as occurs secondarily in dolphins and other toothed whales, may be regarded as a reversion to ancestral conditions in connection with aquatic life, more abundant food, and less need for mastication.

There are some toothless species representing every class of vertebrates. Among fishes may be mentioned the sturgeon, *Acipenser*, and the seahorses and pipefishes. *Coregonus wartmanni*, a whitefish native to Lake Constance in Switzerland, is a toothless member of a large family of toothed fishes (Salmonidae), although this aberrant species has transient embryonic teeth.

Toads, and among urodeles *Siren* at least, are toothless, while frogs have no teeth on the lower jaw. Among reptiles the entire order of Chelonia, which includes turtles and tortoises, are without teeth, although in *Chelonia* and *Trionyx* a reminiscent dental lamina develops temporarily in the embryo, only to fade away as the horny beak becomes ascendant. Several extinct fossil reptiles, for example, *Oudenodon*, *Baptanodon*, and *Pteranodon*, are likewise known to have possessed beaks instead of teeth.

All modern birds are toothless. That this condition was not always the case, however, is shown by the presence of well-developed teeth in *Archae-*

opteryx, and in the Cretaceous birds of Kansas, *Ichthyornis* and *Hesperornis* (Fig. 49). Embryonic teeth, of which there is ordinarily no trace in birds, have been found in the tern, *Sterna*.

Among mammals, monotremes are without teeth, also the edentate *Myrmecophaga* and the pholidote *Manis*, and the large whales (*Mystacoceti*).

A curious instance of hereditary toothlessness in man is reported by Thadani* from Hyderabad Sind in India, where there is an inbred community in which the males never have any teeth. They are called "Bhudas," which means "toothless." This abnormality is accompanied by baldness and extreme sensitivity to heat, and the peculiarity follows the well-known laws of Mendelian inheritance, being a recessive sex-linked character.

All of these widely different toothless mammals, however, furnish embryonic evidence that, with respect to this characteristic, they are degenerate descendants of ancestors with teeth.

(d) *Succession*.—Most of the lower vertebrates are *polyphyodont*, that is, they have a continuous succession of teeth throughout life. This is exemplified particularly in sharks and dogfishes, where the reserve "understudy" teeth may be seen arranged in diminishing rows behind the line in active service at the edge of the jaw. The continuous gradation over the margin of the jaw that separates the serried rows of elasmobranch teeth from the placoid scales of the skin, points unmistakably to a common plan of structure and accounts for vertebrate teeth as modified scales (Fig. 169).

Mammals are typically *diphyodont*, that is, they have a replacement of so-called permanent teeth following the first temporary milk dentition, which allows the young to chew their food at a time when the jaws are too small to accommodate permanent teeth.

Certain marsupial embryos show traces of a still earlier dentition located in the arch between the milk teeth and the lips. Sometimes in exceptional cases mammals produce an additional partial replacement of the "permanent" teeth in late life, making a total of four possible successions, namely, *prelacteal*, *lacteal*, *definitive*, and *post-definitive*, all of which suggests that typical diphyodontism of mammals has been derived from the polyphyodont condition of lower forms. Bolk has pointed out that in diphyodont dentition the replacement comes from a different rudiment than that which gives rise to the first lacteal dentition, so that it is possible to have representatives of both dentitions present and on duty at the same time, whereas in polyphyodontism of the lower forms the succeeding tooth in each case arises from the same germ as its predecessor, thus preventing the intercala-

* *Journal of Heredity*, Feb., 1921.

tion of one active generation of teeth with those of another succeeding generation.

There is, moreover, a tendency among mammals toward a still further reduction to a *monophyodont* condition. Marsupials, for instance, retain all their milk teeth except the last premolars, while certain insectivores, like the moles, *Scalopus* and *Condylura*, never cut their permanent teeth. The toothed cetaceans (*Odontoceti*), and some rodents, as well as the reptile *Sphenodon*, may also be described as monophyodont. Bats and guinea pigs have so far foreshortened the normal procedure of tooth succession as to shed their lacteal teeth *in utero*, coming into the world with their definitive teeth already established.

It is related of Mirabeau, the great orator of the French Revolution, that he was born with teeth already cut, which if true must have been hard on his nurse. Such an abnormality is said to occur as rarely as once out of 15,000 times.

Ordinarily the eruption of milk teeth in man is accomplished in about two years, although it is not unusual for the second milk-molars to come a half year later. The appearance of the permanent dentition begins with the eruption, during the sixth year, of the first molars, just posterior to the last milk teeth. The next year the milk teeth begin to drop out and ordinarily all of them are lost by the end of the twelfth year although an individual may carry some representatives of the lacteal dentition until much later in life. As rapidly as the milk teeth are lost, permanent ones take their places. After the completion of this gradual replacement, two additional molar teeth erupt behind each sixth-year molar, with the last permanent tooth, "wisdom tooth," being fully formed by the twentieth year in most cases.

Milk teeth differ from permanent teeth by their smaller size, whiter color, and by their shape, being more constricted in the neck region and having a greater spread of roots in the case of the back teeth.

(e) **Situation.**—While the teeth in fishes and other aquatic animals occur attached to various skeletal foundations within the mouth cavity, such as the vomer, palatine, pterygoid, parasphenoid, and even on the tongue, on the hyoid and gill arches, in reptiles and mammals they are usually confined to the jaws, although in some snakes, and in *Sphenodon*, they occur also in the roof of the mouth on the vomer and palatine bones.

Teeth of the upper jaw are interspaced with reference to those of the lower jaw. In man the large median upper incisors bite against not only the median but also the lateral incisors of the lower jaw, and every other

tooth of the upper jaw, except the last molars, bites against the corresponding tooth of the lower jaw and also the tooth behind it.

(f) **Attachment.**—The manner in which teeth are attached to their skeletal support is dependent upon the degree to which the roots are developed.

The simplest type of attachment, termed *acrodont* (Fig. 242), occurs in teeth essentially without roots that are held to the edge of the jaw or other skeletal foundation either by fibrous membrane, or ankylosed directly to the bone in shallow pits. Such teeth, which are broken off easily, are *polyphyodont*. In some cases they are hinged on by a ligamentous base and may be folded down when not in use, as in the pike and hake among fishes, as well as in many kinds of snakes. Fishes as well as amphibians are generally *acrodont*.

An improvement over the *acrodont* method is seen in certain urodeles (e.g. *Necturus*) and lizards, where not only the base but one side of the tooth is involved in attachment to a shelflike ledge along the inner margin of the jaw (Figs. 242 and 243). By this method, which is called *pleurodont*, the blood and nerve supply enters at the side, as in *acrodont* teeth, instead of at the tip of the root.

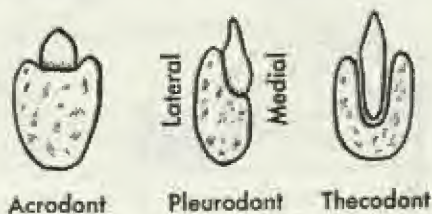


Fig. 242. Types of attachment of teeth to jaws. (After Wiedersheim.)



Fig. 243. Medial view of a lizard jaw bearing pleurodont teeth. (After Hiltzheimer.)

The highest and most efficient type of tooth has well-developed roots set in bony sockets in the jaw, a method of attachment known as *thecodont* (Fig. 242), by which the capillaries and nerves enter the pulp cavity through the open tips of the hollow roots.

Some reptiles are *thecodont*, alligators and crocodiles particularly, but this type of tooth attachment is more characteristic of mammals, in some of which the teeth have progressed much beyond the primitive grasping function, and consequently require a stronger anchorage than is afforded by either the *acrodont* or *pleurodont* methods.

The incisor teeth of gnawing rodents are so deeply set in bony sockets of the jaws that they become very effective tools, as for example the incisors of the gopher *Geomys* (Fig. 244). The beaver *Castor*, in its engineering operations, can cut down large trees with such teeth.

(g) **Movement.**—Various types of movement for teeth set in jaws are made possible by the muscles of mastication. The commonest type is vertical,

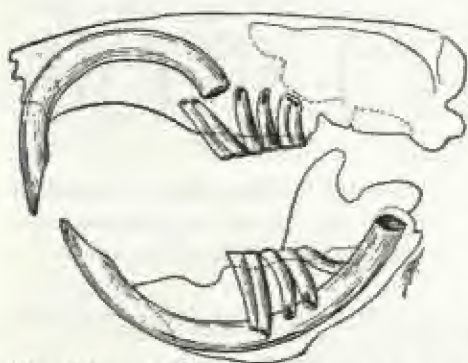


Fig. 244. Teeth of a rodent, *Geomys*, showing diastema, or toothless space in jaw between incisors and molars. (After Bailey.)

cal, or *orthal*, movement, which consists in lifting up the lower jaw. Just as in a nutcracker, the farther back toward the angle of the jaw the work is done, the more powerful is the effect.

In carnivores the back teeth cut past each other like the blades of a pair of scissors. Ungulates which chew the cud with a sidewise motion have a lateral method of jaw movement, while horses, elephants, rodents, and some other herbivorous animals practice a "fore and aft"

movement. In all of these movements the effective use of the jaw involves the teeth on one side at a time, those of the opposite side being temporarily not in contact.

Snakes with their sharp backward-projecting prehensile teeth use the fore and aft movement to advantage in relentlessly passing along struggling prey down the throat. In fact it works so automatically that a snake finds it difficult to eject a mouthful, once started in the proral-palinal mill.

In the higher vertebrates still other modifications in the movement of the jaws may be noted. Dr. Hooton observes that "with the shortening of the canines the human stock developed certain rotary movements of mastication which may be observed in any gum-chewing stenographer."

(h) **Differentiation.**—According to their degree of differentiation, teeth are described as homodont and heterodont. Teeth when practically all alike are called *homodont*, but if they are differentiated to serve a variety of uses, such as gripping, tearing, cutting, or crushing, they are known as *heterodont*.

The teeth of primitive water-dwelling vertebrates are commonly homodont, since aquatic animals do not chew. They are usually pointed or cone-shaped and adapted to serve as prehensile organs. Ordinary vertebrates with homodont teeth gulp their food whole.

In evolutionary history, heterodontism arose along with experimenting upon a variety of foods and with the consequent occasion for chewing. The mammal-like therapsid reptiles and the mammals themselves are heterodont. The back teeth near the hinges of the jaws where the leverage is greatest become modified into grinding *premolars* and crushing *molars*, or "cheek teeth," while the front teeth, notably in the case of rodents, become specialized into cutting chisels, or *incisors*, to divide the food into morsels of convenient size for the grinding mill of the back teeth. Probably the

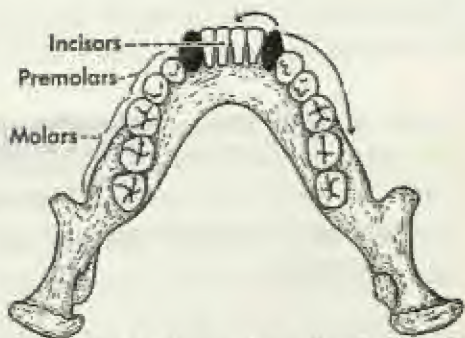


Fig. 245. A human jaw, showing by arrows the two general types of differentiation in teeth from the primitive pointed canine teeth represented in black.

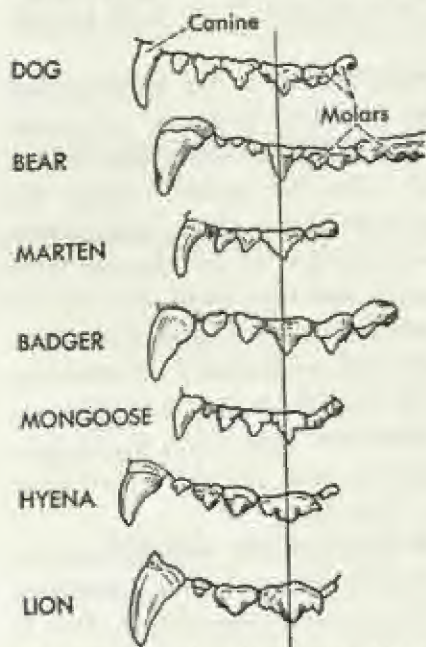


Fig. 246. Teeth of the upper left jaw of various carnivores. The vertical line passes through the fourth premolars, or carnassial teeth. (After Boas.)

former case the sharp edges of certain grinders fit past each other like shears, for cutting up animal food, the grasping canines are prominent, and the back molars tend to become degenerate. It is the fourth premolars

or *incisors*, to divide the food into morsels of convenient size for the grinding mill of the back teeth. Probably the most ancestral and least changed of all heterodont teeth are the cone-shaped *canines*, between the incisors and premolars, which resemble the pointed grasping teeth of the homodont type. On either side of the canines, as a point of departure, modification has taken place progressively and in divergent fashion, as indicated by the arrows (Fig. 245), on the one hand toward the flattened, more chisel-like type of the incisors, and on the other, toward that of the flat-topped premolars and molars.

Homodontism in the dolphin and other toothed whales is shown to be secondary by the fact that a fossil ancestral whale, *Zeuglodon*, was heterodont.

The heterodontism of carnivores (Fig. 246) is characteristically different from that of herbivores. In the



Fig. 247. Selenodont dentition, or molars with crescentic surfaces of hard enamel.



Fig. 248. Grinding surface, partly worn, of right upper molar of African elephant. (After Owen.)

on the upper jaws and the first molars on the lower jaws which have developed this special tearing or shearing ability, for which reason they are called *carnassial* teeth. In the herbivore type of heterodont dentition the more anterior cheek teeth show degeneration, the canines being suppressed, while the posterior grinders near the hinge of the jaw become flattened and enlarged so as to crush seeds, fruits, nuts, and herbage of all sorts successfully.

The molars of ruminants present a flat grinding surface further diversified by crescentic ridges of projecting enamel, alternating with softer dentine. Since the dentine wears away more rapidly than the enamel ridges, the enamel is constantly kept with sharp edges, and at the same time a rasp-like abrasive surface on the grinding teeth is maintained. Such crescentic-surfaced teeth are said to be *selenodont* (Fig. 247). Similar enamel ridges are present on the molars of elephants, the arrangement of which in transverse lines instead of in crescents makes a washboard-like pattern, described as *lophodont* (Fig. 248), that is particularly effective in connection with the palinal or from behind forward movement of the jaws.

In man and some other mammals, the grinding surface of the molars is raised slightly into separate rounded tubercles and, being entirely covered with enamel, wears away more evenly. This is described as the *bunodont* type of teeth.

It is illuminating to know that some of the ancestral elephants, *Palaeomastodon* for example, were bunodont, while their more specialized descendants of today have become lophodont.

Finally, to add two more "dents" to this descriptive vocabulary of the teeth, the term *brachydont* applies to teeth with short crowns and comparatively long roots, as in man, while the term *hypodont* characterizes teeth

with short open roots and long crowns, such as are found in the dentition of the horse, in the tusks (incisors) of elephants, and the canines of boars.

(i) **Dental Formulae.**—In the case of different species that have heterodont teeth, it is useful to express the degree of their diversity in some convenient and compact form. This is accomplished by means of *dental formulae*. For example, the permanent dentition of man may be expressed as follows: $\frac{2.1.2.3}{2.1.2.3}$, in which the figures above the horizontal line indicate in order from left to right the number of incisors, canines, premolars, and molars on the right side of the upper jaw, while the figures below the line stand for the corresponding teeth in the lower jaw. It is unnecessary of course to indicate the teeth on the left side, which are like those on the right side except in reverse order.

The short-tailed monkeys (Catarrhini) of the Old World have the same dental formula as man, but the long-tailed monkeys (Platyrrhini) of the New World have an additional premolar all around, making the formula $\frac{2.1.3.3}{2.1.3.3}$, with a total of thirty-six.

Some other dental formulae are as follows:

opossum $\frac{5.1.3.4}{4.1.3.4}$,	dog $\frac{3.1.4.2}{3.1.4.3}$,	pig $\frac{3.1.4.3}{3.1.4.3}$,
kangaroo $\frac{6.0.1.4}{2.0.1.4}$,	cat $\frac{3.1.3.1}{3.1.2.1}$,	horse $\frac{3.1.4.3}{3.1.4.3}$,
basic placental $\frac{3.1.4.3}{3.1.4.3}$,	skunk $\frac{3.1.3.1}{3.1.3.2}$,	cow $\frac{0.0.3.3}{3.1.3.3}$,
bat $\frac{2.1.0.4}{3.1.0.5}$,	squirrel $\frac{1.0.2.3}{1.0.1.3}$,	sheep $\frac{0.0.3.3}{3.1.3.3}$,
bear $\frac{3.1.4.2}{3.1.4.2}$,	mouse $\frac{1.0.0.3}{1.0.0.3}$,	

In herbivores the canine teeth are missing or much reduced, leaving a toothless space, the *diastema* (Fig. 244), between the incisors and the premolars. The canines are relatively so small in the horse that a practical diastema exists, furnishing the space where the bits of the bridle are held.

(j) **Origin of the Molars.**—There are at least two theories to account for the origin of the molar teeth in mammals.

First, the *concrescence theory* of Röse and others assumes that they are the products of the fusion of separate primitive cone-shaped teeth. The posterior teeth in the jaw of *Sphenodon* offer evidence in support of this point of view.

The other and more widely accepted explanation is the *differentiation theory* of Cope and Osborn, which postulates the budding out and growth of additional contact surfaces, or *cusps*, upon the crown of an originally conical tooth (Fig. 249). This theory is based largely upon evidence presented by the ancestral teeth of fossil mammals. It is quite possible that both theories will be of use, since they are not mutually exclusive, in reaching a satisfactory conclusion in the matter.

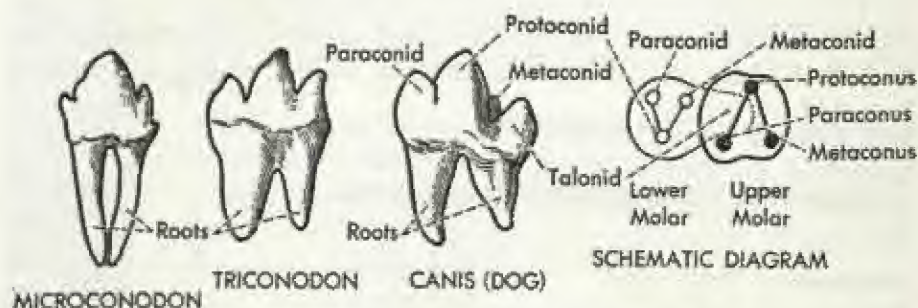


Fig. 249. Plan of molar teeth. Anterior is to the left in each case. (After Osborn.)

The addition of two such cusps gives rise to the *tritubercular tooth* which is the typical molar of mammals generally from the earliest representatives down to Eocene times. Even today the mole *Chrysochloris* and certain other insectivores, as well as the opossum *Didelphys*, and some lemurs, exhibit this ancestral tritubercular type, which is well adapted to the business of crushing insects.

The three cusps of a tritubercular molar are arranged in the form of a triangle. Molars of the *lower jaw* have a more lateral cusp, the *protoconid*, medial to which are the two secondary cusps, the *paraconid* in the anterior position and the more posterior *metaconid*. The corresponding cusps on molars of the *upper jaw* are indicated by the termination—*us*. Thus in a molar of the upper jaw there are a medial *protoconus* and two more lateral cusps, an anterior *paraconus* and a posterior *metaconus*. This means that the orientation of the triangle of cusps on the upper jaw is the mirror image

of that on the lower jaw. The seemingly elaborate terminology here employed is indispensable to the student who would make a study of the story of mammalian teeth. The addition of extra cusps on more highly developed molars may bring the total number to a maximum of six. Molars of the lower jaw, for example, elongate somewhat through the development of a posterior extension, the *talonid* or "heel," which may bear two or three extra cusps. Because the teeth of the upper jaw alternate with those of the lower jaw in most cases, the protoconus usually strikes against the talonid of the corresponding lower-jaw molar.

(k) **Unusual Teeth.**—Sometimes a pair of teeth develop excessively, forming *tusks*. These may be either incisors or canines and are more likely to appear in the male than in the female, although both sexes of elephants and walrus have tusks.

The largest known tooth is the tusk of an extinct mammoth, *Archidiskodon*, that is in the American Museum of Natural History in New York City. It weighs over 250 pounds and is more than sixteen feet in length.

The wild boar with tusks formed from modified canines of the lower jaw, strikes upward, while the male "dugong," *Halicore*, or sea-cow of the Red Sea, makes the effective blow from above downward with tusks evolved from the upper incisors. In both sexes of *Phacochoerus*, the wart hog of Africa (Fig. 67b), there are four upward curving tusks, which are the transformed canines of both jaws, those of the upper jaw bending sharply to pierce the upper lip.

In general, tusks, as well as the prominent cutting incisors of rodents, retain at their base a large opening into the pulp cavity, thus insuring an abundant blood supply and consequent continued growth to compensate for the wearing away of the crown to which these exposed teeth are subjected. Such teeth in a way may be likened to angora hair in their manner of continuous growth.

The male narwhal, *Monodon* (Fig. 75c) has lost all its adult teeth except an upper left one which is prolonged enormously into a formidable twisted pikestaff that may reach seven to nine feet in length. The saw-fish, *Pristis* (Fig. 20c), which is not a mammal but a selachian, carries a similar weapon in the form of an elongated snout, or *rostrum*, with laterally projecting teeth along its sides.

In rodents the chisel-like incisors are faced with enamel only on the anterior surface. Because the enamel is much harder than the dentine that is posterior to it, these incisors wear away more rapidly behind than in front, constantly leaving sharp cutting beveled edges of enamel. When a rodent is so unfortunate as to lose an incisor of either jaw, leaving the

incisor of the other jaw with no tooth to wear against, the animal usually meets eventual death by starvation because the surviving tooth, unhindered in growth, often reaches so great a length that the mouth can no longer be properly closed and feeding becomes impossible.

Among poisonous snakes a pair of anterior teeth may develop into *fangs*, which are teeth that are either grooved or hollow. Whenever a fang is struck into another animal the secretion of the poison gland at the base of the fang is pressed out through the hollow or groove into the wound (Fig. 230).

A so-called *egg tooth*, composed largely of dentine, is present as a transitory structure in the embryos of snakes and lizards which are imprisoned within an eggshell. It is situated in a median position and projects forward at the tip of the upper jaw. The young reptile uses it like a can-opener to hatch itself out of the imprisoning shell. According to Röse a pair of egg teeth are present at first in the embryo of the viper, *Vipera*, but only one becomes developed sufficiently to be of service, and this is shed soon after hatching.

There is a *corneal egg "tooth"* of horny texture on the tip of the beak of many unhatched birds. Although not homologous with the egg tooth of

snakes and lizards, it nevertheless serves the same purpose. It may sometimes be seen still adhering to the tip of the beak of young chicks which have just hatched into the world (Fig. 250B). A similar horny temporary emergency tool is present in *Sphenodon*, the crocodiles, and turtles, as



Fig. 250. Transitory corneal egg-tooth which is used as a "can opener" in hatching out of the shell. A, alligator; B, bird. (After Hiltzheimer.)

well as in the monotremes, which are the only mammals that hatch out of an eggshell.

(1) **The Trend of Human Teeth.**—The teeth of ancient man show certain differences from those of man today, which possibly give some suggestion as to the direction of the future evolution of human dentition. The jaws in which the teeth are set are becoming shorter and less prognathous, with the result that the teeth of modern man are more crowded and less regular in eruption. Also decay, or *caries*, is more common in the teeth of modern civilized man than in the teeth of his prehistoric ancestors, where it was practically unknown. Wiedersheim reports on evidences of decay in teeth after an examination of a large number of skulls from various extensive museum collections, as follows: Eskimos, 2.5 per cent; Indians, 3–10

per cent; Malays, 3-20 per cent; Chinese, 40 per cent; Europeans, 80-100 per cent.

In primitive man the upper incisors came into opposition, edge to edge, with the lower incisors, and were frequently worn flat in consequence, while in modern man there is a tendency for them to shut past each other like the blades of a pair of shears, and thus to maintain a cutting edge.

The "wisdom teeth," or the third molars, so-named by Hippocrates, the Father of Medicine, are apparently doomed teeth. They are the last to appear and the first to go. Frequently they remain uncut, or do not develop a grinding surface. In prehistoric man, however, they were plainly in evidence, and they are unusually well developed in negroes, mongols, and aboriginal Australians.

The upper lateral incisors and the second molars also show evidences of being degenerate structures, failing to appear in a considerable number of cases.

Davenport * writes of human teeth as follows: "At birth the front teeth are always formed with enamel and dentine and so the trouble that is associated with these marvelous organs begins. . . . The teeth are cut in discomfort, they decay and treatment brings pain, they are pulled out with pain. . . . Let us be happy that we have not so many teeth as the sharks."

IV. PROGRESSIVE ZONE

1. Pharynx

The pharynx includes the stretch of digestive highway from the posterior part of the mouth cavity to the beginning of the esophagus. While its actual extent is relatively small, its diversity of function, and consequently the degree to which it is modified in various vertebrates, is very great.

The pharynx serves as a point of departure for describing the respiratory system, since among fishes and amphibians it is the region of the gills, as well as the point of origin for the swim bladder of fishes and the lungs of land animals. This aspect of the pharynx will be taken up in the chapter on Respiration. The description of the numerous pharyngeal glands, thyroid, parathyroids, thymus, epithelial corpuscles, and ultimobranchials, will also be deferred until the chapter on endocrinal glands.

Traveling through the gateway of the pharynx are two quite different streams of material, namely food and oxygen. In fishes they enter the mouth together (Fig. 251A), and proceed in parallel course without mutual inter-

* *How We Came by Our Bodies*, Henry Holt and Co., 1936.

ference, food passing straight to the esophagus where it continues on its way, while oxygen, dissolved in water, passes out over the gills hanging in the lateral gill slits, which like portholes pierce the sides of the pharynx. The paired nasal pits on the snout of a fish do not open into the mouth cavity, and have nothing to do with the pharynx or with breathing.

In amphibians, the first land forms that possess lungs and breathe free air, the nasal pits deepen until they break through into the mouth cavity, thereby forming a pair of respiratory passage-ways. The openings into the mouth cavity are the *internal nares*, or *choanae* (Fig. 251b). These allow air to pass to the lungs without the necessity of opening the mouth, thereby exposing its mucous lining to disastrous drying up. Free air is taken into the mouth cavity through the choanae with the mouth closed. After valves in the external nares have closed, the floor of the mouth is raised. Thus the air is forced back into the lungs, a process which would be quite impossible with the mouth open, as the air could then escape in the wrong direction.

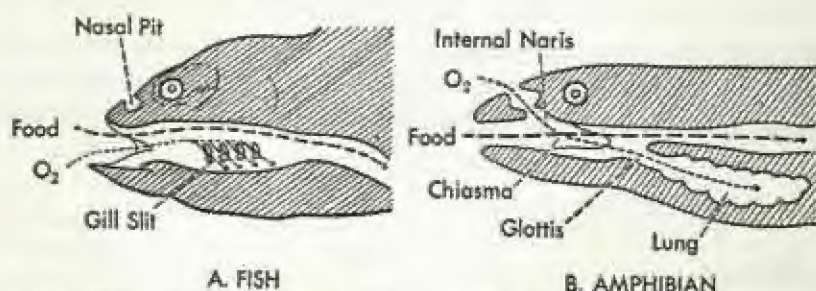


Fig. 251. Diagrams of the evolution of the pharyngeal chiasma. For man refer to Fig. 252. (After Wiedersheim.)

Embryonically the lungs are ventral outgrowths from the floor of the pharynx, and thus, while the food takes a straight course from mouth to esophagus as in fishes, air, entering the nostrils dorsally, crosses the path of the food and is forced ventrally into the lungs.

Vertebrates above the amphibians, that is, reptiles, birds, and mammals, have developed a hard palate, or secondary roof of the mouth, which forces the choanae backward so that the crossing of the ways is transferred from the oral cavity to the pharynx. This crossing is known as the *pharyngeal chiasma*.

In mammals this arrangement has been accompanied by the establishment of various anatomical modifications (Fig. 252) that, like traffic officers at a busy street crossing, regulate the traffic and prevent confusion, although adding materially to the expense of maintenance. The *epiglottis*,

for example, is introduced as a trapdoor device to guard the entrance into the trachea so that food passing by shall not go the wrong way.

It may be pointed out that if in man air had been made to pass through the chin instead of the nose, thus avoiding the pharyngeal chiasma entirely, at least some present troubles would have been eliminated, although with such a drastic change other difficulties might have been introduced. In any case the pharyngeal chiasma clearly stresses the fact that our anatomical machinery is the inevitable result of many successive modifications rather than being formed *de novo* from blueprint specifications. A moral to be gained from comparative anatomy, as well as from other aspects of life, is that one should seek to make the best of his inheritance, whatever it is, rather than vainly to regret not having been endowed with perfection in the beginning. The acquisition of adaptations by successive stages, each of which is always *dependent upon what has gone before*, is not only the method invariably followed in the phylogenetic establishment of species, but it is also the only way that any anatomical structure in an individual comes into being embryonically.

In man the pharynx is shaped somewhat like a funnel about five inches deep. It extends from the base of the skull to the level of the sixth cervical vertebra, where it narrows into the esophagus. Its three merging irregular cavities, one below the other, may, for purposes of description, be designated as the nasopharynx, oropharynx, and laryngopharynx.

The upper *nasopharynx* (Fig. 252), which is not concerned with alimentary traffic but is entirely respiratory in function, lies dorsal to the soft palate. In general it retains a definite contour, since its bony walls are practically inflexible. On either side of the nasopharynx opens an *Eustachian tube* from the air chamber of the middle ear. These tubes are the morphological successors of the second pair of gill slits, or the *spiracles*, between the mandibular and hyoid arches of ancestral aquatic forms.

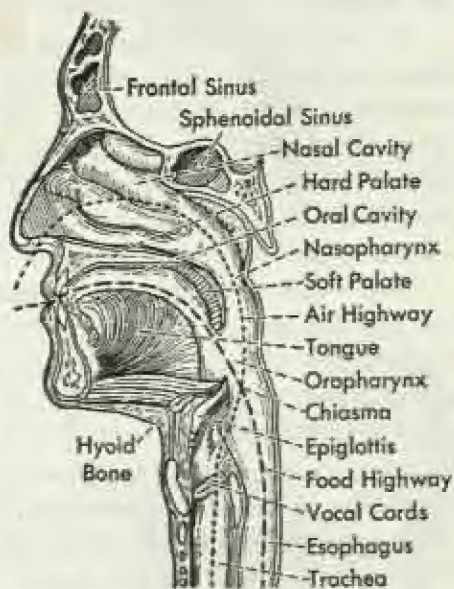


Fig. 252. Sagittal section through the head and throat of man, to show the pharyngeal chiasma. The position of the chiasma here is pushed back as a result of the development of the hard palate.

The *oropharynx*, posterior to the nasopharynx, communicates through the *isthmus of the fauces*, or the posterior exit of the oral cavity, directly with the cavity itself. Forming the ventral wall of the oropharynx is the base of the tongue that here assumes a vertical position, practically reducing the oropharynx to a transverse slit when the mouth is closed.

On the sides of the oropharynx are two masses of glandular or lymphoid tissue, the *palatine tonsils*, while upon the posterior wall of the nasopharynx is still more of this peculiar tissue, the *pharyngeal tonsils*, commonly known when enlarged as *adenoids*. On the vertical face of the base of the tongue, behind the sulcus terminalis, are the *lingual tonsils* (Fig. 233). An incomplete ring of tonsillar tissue, therefore, surrounds the pharyngeal passageway, of which the part made up of palatine tonsils is the most prominent.

Along with the tonsils there is developed throughout the entire pharyngeal region a variety of adaptive glandular and lymphoid structures having a wide range of functions, and forming the seat of so many complications and troubles, both structural and physiological, that physicians and surgeons specializing in this field alone, have their busy hands full.

The *laryngopharynx*, continuous with the oropharynx, is the indefinite lower part of the pharynx between the soft palate and the esophagus. It includes the critical region of the pharyngeal chiasma, and surrounds the larynx, or voice box. Except during the passage of food, which slips past down either side of the closed *glottis*, the laryngopharynx is collapsed into a narrow slit.

Thus it will be seen that the pharynx as a whole, like a colonial kitchen, opens into several adjoining spaces. It has communication in fact through seven different openings, namely, two choanae, and two Eustachian tubes in the nasopharynx; the isthmus of the fauces in the oropharynx; and in the laryngopharynx, the glottis and the esophageal opening.

2. Esophagus

Over the entrance of the esophagus might well be written Dante's immortal line: "All hope abandon, ye who enter here," for in its course the muscles of its walls pass from voluntary to involuntary nerve control. Of all the vertebrates, some birds and the ruminant mammals are exceptional in that they have voluntary muscle fibers extending the whole length of the esophagus and are, therefore, able to regurgitate the food at will. The so-called "milk" which some birds regurgitate is used to feed their young. Ruminants, on the other hand, regurgitate their hastily swallowed food for more prolonged chewing.

The esophagus, a short comparatively unmodified part of the digestive

tube between the pharynx and the stomach (Fig. 253), is primarily a sphincter, the office of which is to forward food by peristalsis along its course to a point beyond normal control. The peristaltic action of the walls of the esophagus is well shown by a horse drinking at a brook, for the gulps of water taken in have to travel up hill along the neck and their passage is externally visible. In the case of a snake the violent peristalsis necessary in swallowing a comparatively large morsel of food, such as a frog, is supplemented by the muscles of the body wall.

When not in use the esophagus collapses to modest dimensions, but upon occasion it is capable of great temporary distension. There are certain fishes that can even swallow another fish larger than themselves (Fig. 254). In many vertebrates the inner lining of the esophagus is characterized by expansive longitudinal folds that allow for a sudden increase in diameter during the act of swallowing, but at other times contract so that the tube may occupy a minimum of space.

The inner lining of the esophagus of marine turtles is beset with backward-projecting horny papillae, which enable them more easily to swallow the slippery seaweeds upon which they habitually feed.

The length of the esophagus is dependent largely upon the presence or absence of a neck. In frogs and toads the neck is reduced to a minimum so that a fly entering the mouth of one of these animals finds itself almost immediately landed in the stomach, whereas in long-necked animals, such as the giraffe for example, the esophageal adventures of food are much more extended. In adult man the length of the esophagus is approximately

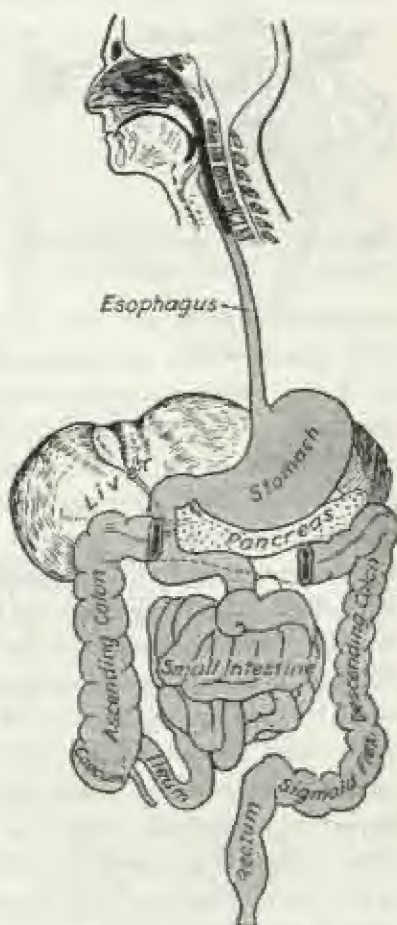


Fig. 253. General diagrammatic view of the digestive system in man. The liver has been tipped anteriorly to show the gall bladder and common bile duct. The transverse colon has been cut to show the duodenum (the beginning of the small intestine), but its course is indicated by dotted lines. (After Cunningham.)

fourteen inches, the lower end piercing the diaphragm to enter the body cavity before joining the stomach. It is only this short portion within the body cavity that is provided with a serosa layer of tissue outside the muscular and mucosa layers.



Fig. 254. A fish that has swallowed another fish larger than itself.

A noteworthy differentiation of the esophagus in birds is a lateral enlargement known as the crop (Fig. 255), which may serve simply as a convenience for the temporary storage of food hastily secured in the presence of enemies or competitors, as in the case of seed-eaters generally, or may be supplied with glands which act chemically upon the food eaten. Pigeons produce a cheesy nutritious substance from the lining of the crop, called "pigeon's milk," that is fed to nestlings by regurgitation. The tropical hoactzin, *Opisthocomus*, has a muscular crop which works mechanically upon the food that finds lodgment in it. A chicken going to roost with its crop filled with corn, falls asleep unhampered by the continuous effort of picking up food and "feeds" all night long while resting, as the crop, like the hopper of a gristmill, releases its contents automatically and periodically to the glandular stomach and grinding gizzard as needed.

Among the lower vertebrates any external line of demarcation between the esophagus and stomach is either absent or vague, but in birds and mammals there is usually a definite point of transition. In many cases it is easier to gain entrance to the stomach from the esophagus than to escape from the stomach into the intestine.

3. Stomach

The stomach is a conspicuous enlargement of the digestive tract lying between the esophagus and the intestine (Fig. 256). Originally, as in some

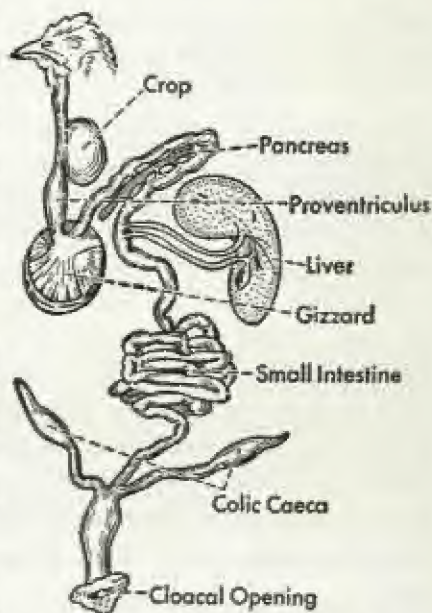


Fig. 255. Digestive tract of a hen.

fishes and salamanders, it is spindle-shaped and arranged to conform with the general contour of an elongated body, but in higher vertebrates it becomes saclike in shape, assuming a somewhat transverse position in the body cavity. Between these extremes may be found many gradations of form and position.

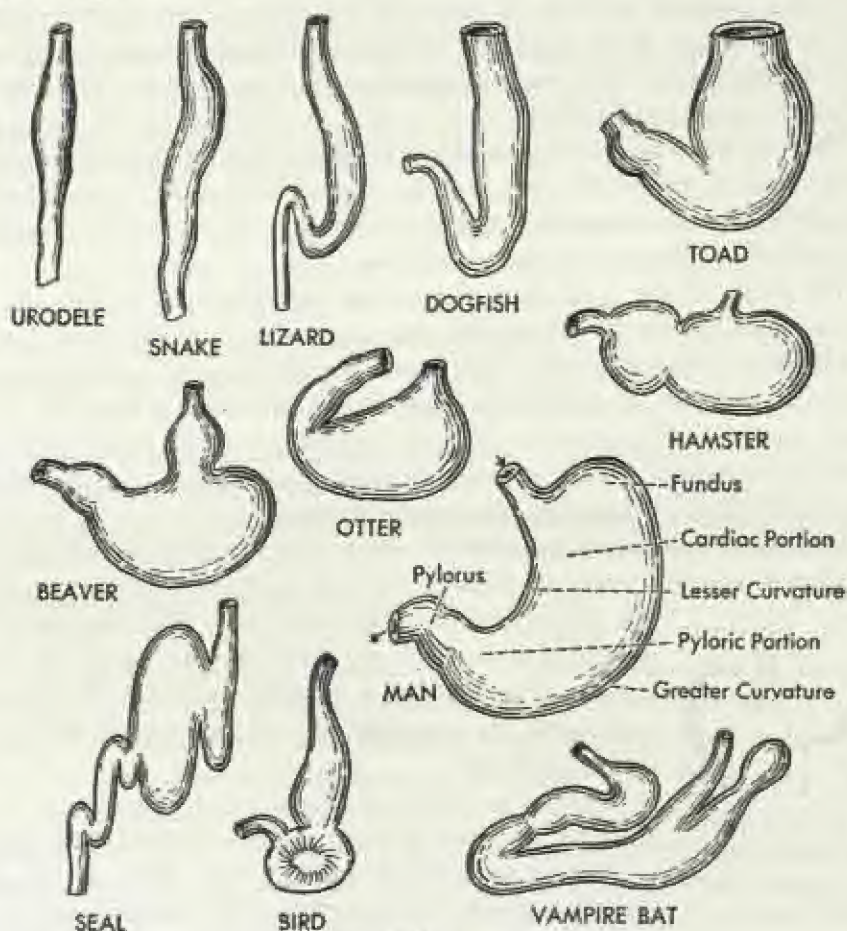


Fig. 256. Different stomachs.

The stomach of the dogfish, for example, instead of being a primitive straight spindle-shaped enlargement with the entrance and exit at opposite ends, is doubled back in the form of a J-shaped tube. Stomachs of similar shape occur also in the flounder, haddock, salmon, carp, sturgeon, sole, and many other fishes. In fishes such as the perch, smelt, herring, bullhead, and whiting, the loop becomes fused along its inner bend in such a way that a bag-shaped pouch, or *fundus*, is formed with the entrance and exit brought

near together at one side. This type of a stomach, when shifted into a transverse position, is much like that of man, with a *lesser curvature* on the upper side between the entrance and the exit, and a *greater curvature* forming the larger contour around the outer margin or elbow of the stomach.

The entrance to the human stomach is somewhat larger than the exit and is less distinctly marked off, although the lining of the digestive tract itself in the region of the esophagus is easily distinguished from that of the stomach, even when the external transition from one part to the other is extremely vague and indefinite.

The exit from the stomach is closed by the *pylorus*, or *pyloric valve*, a fold of mucous membrane reinforced by a sphincter muscle, which relaxes temporarily for the release of food into the intestine only when the stimulative password of proper acidulation is given.

The walls of the stomach are muscular enough to insure the active movement of the food-mass around and around by peristalsis until it has been reduced, through mixture with glandular secretions, to a suitable consistency and degree of acidity. In other words, the food is kneaded and mixed under muscular pressure. Then, as it is presented at the closed pylorus, the sphincter muscle relaxes, allowing small successive amounts of the mixture, called *chyme*, to slip through into the intestine.

Amphioxus and larval cyclostomes, which have not gone far enough in evolution to develop peristaltic muscles, have, according to Schimkewitsch,

the entire digestive tube lined with cilia, the mission of which is to keep the food moving along. In the human fetus also, as a possible reminder of whence man came, the posterior part of the stomach lining is clothed with cilia.



Fig. 257. So-called "hour-glass stomach" in man. (After Wiedersheim.)

There is a tendency for the stomach to become differentiated into two or more regions, distinguished from each other by location and function. Thus, in the J-shaped stomach of the dogfish which involves half the entire length of the digestive tract one speaks of a

cardiac limb and a *pyloric limb*, while in certain mammals, the mouse for example, a constriction in the middle part of the stomach marks off a cardiac chamber from a pyloric chamber.

Medical literature contains references to the occasional occurrence of so-called "hour-glass stomachs" in man (Fig. 257), which bear a strong resemblance to the two-chambered stomachs of mice. Certain monkeys (*Hylobates* and *Semnopithecus*) show the same feature. Whether such unusual structures in man are pathological or ancestral is uncertain.

An extreme subdivision of the stomach is reached by the ruminants, which have four "stomachs" (Fig. 258). The first in order is the "paunch," or *rumen*, which is a spacious storage bag for the temporary reception and fermentation of grass or herbage upon which ruminants feed. Microorganisms present in the rumen of domestic cattle, and possibly other ruminants, act upon simple nitrogenous compounds to synthesize proteins as well as sufficient quantities of the B-complex vitamins to supply the dietary needs of these vertebrates. From the rumen the food is passed over into the "honeycomb stomach," or *reticulum*, that, as its name indicates, is lined with many shallow pits. When leisure from prehensile feeding comes, food which was hurriedly swallowed with little mastication is regurgitated into the mouth for rechewing. This material, coming in part from the rumen and in part from the reticulum, is known as the "cud." It includes roughage, such grains as happen to be trapped in the roughage, and a considerable quantity of water which facilitates the passage of the

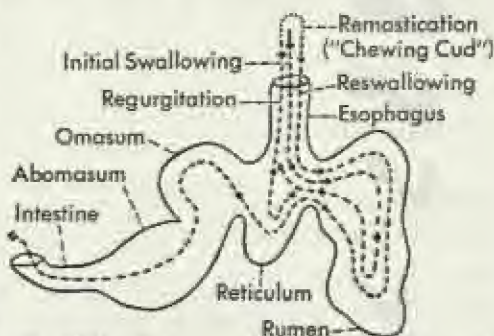


Fig. 258. Diagram of a ruminant stomach, with broken lines showing the course of the food.

cud up the esophagus. During the first few chewing movements the animal swallows most of the liquid brought up. After remastication and a thorough mixing with saliva, the food is again swallowed and passes once more into the rumen. Then another cud is regurgitated, thus beginning a new cycle of rumination. Most of the food that has been thoroughly chewed and mixed with liquid soon passes into the reticulum and then shortly into the *omasum*, or "manyplies stomach." This third chamber is lined with numerous folds and communicates directly with the true "glandular stomach," or *abomasum*, where the food is mixed with gastric juices and chemically modified before being forwarded into the intestine. In "water cells" in the walls of the rumen and reticulum, camels are able to store reserve water which enables these desert animals to endure prolonged periods of dryness.

The vampire bat, *Desmodus*, exhibits a peculiar adaptation with reference to its blood-sucking habits, the fundus of the stomach being drawn down into a deep elastic pouch (Fig. 256). When a vampire fastens on to a warm-blooded victim it can fill this spacious reservoir with blood until the entire body is swollen in consequence.

The cardiac and pyloric regions of the stomach in birds have become

separated into chambers very unlike each other in character (Fig. 255). The cardiac chamber, or *proventriculus*, which opens into the *gizzard*, becomes a *glandular stomach*, where the food undergoes some preliminary maceration and chemical modification before reaching the gizzard through which it passes to the intestine. The gizzard has a thick muscular wall and is lined with a hard secreted layer. In this muscular mill food is ground up, instead of by means of teeth as in mammals. Gravel, or "gizzard stones," retained temporarily within the gizzard cavity, aids in the process of food attrition. The whole device is a part of the general program of centralization of organs which the birds, as adapted flying machines, have evolved. The highest differentiation of the gizzard is reached in seed-eating birds, and the least in birds of prey.



Fig. 259. X-ray of the contents of a cat's stomach at successive intervals after being fed with bread and milk and bismuth substrate, which is opaque to the X-ray. (After Cannon.)

Among reptiles the crocodilian stomach approaches that of birds in its differentiation, since a gizzard-like pyloric chamber receives the food after it passes over from the glandular cardiac sac, which corresponds to the chemically functioning stomach of other animals.

There are at least three general functions performed by the vertebrate stomach, namely, storage, mechanical manipulation, and chemical modification.

The advantages of *food storage* are obvious. Among lower sedentary creatures, like sponges and clams for example, there is no provision for food storage, in consequence of which feeding is practically a continuous process. With the necessity of hunting for food, rivalry for daily bread and adventurous escape from devouring enemies become more and more the constant daily program of animal existence. The necessity for seizing a sufficient supply of food, when it is available, in a minimum of time and then retiring to safety or engaging in other activities, is apparent. By periodic voluntary filling of a storage chamber like the stomach with food, opportunity is left for other activities at the same time that the involuntary machinery of the body is faithfully attending to the digestive processes with meticulous deliberation and care.

The function of *mechanical manipulation*, or peristalsis, has already been mentioned. By this means the muscular walls of the stomach knead the food-mass around, mixing it with digestive secretions. The movement

may actually be seen upon a fluorescent screen when an animal like a cat, whose food has been mixed with barium sulphate or some other substance that is opaque to X-rays, is exposed to their action (Fig. 259).

The function of *chemical modification* is dependent upon the presence of glands in the lining of the stomach, which produce secretions of various kinds. In the region of the fundus, *gastric glands* are most numerous. These produce hydrochloric acid and three kinds of enzymes, namely, *pepsin*, *rennin*, and *gastric lipase*, which do preliminary service in the chemical reduction of proteins and fats. Pepsin, acting only in an acidulated medium, breaks down protein foods to simpler compounds; rennin coagulates the protein *casein*, a constituent of cheese, out of milk, rendering it capable of being changed by pepsin into simpler substances that are prepared to undergo other necessary changes farther along in the digestive tract; finally, gastric lipase begins the work of splitting up fats into soluble fatty acids and glycerine.

It is the hydrochloric acid generously produced by the gastric glands of dogs that enables them to dissolve bones which they crunch and swallow.

The protein lining of the stomach itself is not digested by its own secretions because its component cells are living and thus resistant to enzymatic action. It is only when a cell is dead that it yields to destruction by gastric juices. This explains how a tapeworm can live and prosper while bathed in the digestive gastric secretions of its host.

Man is the only animal that hastens the reduction of food to soluble form by cooking it.

V. DEGRESSIVE ZONE

The intestinal stretch of the digestive tract is a long lane with many turnings. In higher vertebrates it is differentiated into the *small intestine*, or degressive zone, in which food substances passing through are diverted into the blood stream, and a shortened part, usually of somewhat greater diameter, known as the *large intestine*, constituting the egressive zone from which the unutilized residue of the food-mass is ejected.

1. The Small Intestine

All other regions of the digestive tract are subsidiary in function to the small intestine. It is here that the food-mass, which has undergone chemical and mechanical modification on the way, is finally converted into sufficiently soluble form to be passed over into the blood stream by diffusion, whence it is finally distributed to the uttermost needy cells of the body.

The straight, comparatively short intestine of cyclostomes, undifferentiated into small and large regions, has its absorbing surface increased by a *typhlosole*, an internal fold including mucosa and submucosa, which makes only a few spiral turns in the entire length of the intestine (Fig. 211).

In elasmobranch fishes the typhlosole, making numerous spiral turns, is much longer than the intestine, with the result that it becomes twisted into a *spiral valve* (Fig. 212). This makes an enlarged surface within a very compact space for the diversion of food, since the intestine is no longer than the J-shaped stomach and is not bent.

A spiral valve is also present in the intestine of dipnoans, certain ganoids, and at least one exceptional teleost (*Chenocentrus*). Twisted *coprolites* (fossil feces), found with the bones of ichthyosaurs, indicate that these extinct reptiles might also have been equipped with a spiral valve device that moulded the feces into a twisted shape.

The ganoids show a different method of increasing the intestinal surface, by means of *pyloric caeca* which are saclike diverticula at the beginning of the small intestine (Fig. 214). Both spiral valve and pyloric caeca are present in the sturgeon, *Acipenser*, although poorly developed.

The next step in the evolution of the small intestine is found in the teleost fishes, which have given up the spiral valve idea and gone over entirely to the elaboration of pyloric caeca. In some of the bony fishes these structures form a large tuft of tubules, occupying considerable space within the constricted body cavity (Fig. 214). They vary in number from one in the ganoid *Polypterus*, and the sand-lance, *Ammodytes*, to over two hundred in the mackerel, *Scomber*.

The distinction between the small and large intestine begins with amphibians, also the diversification of the inner surface of the small intestine by villousities, which reach their greatest differentiation in the small intestine of mammals. In amphibians the entire lining of the digestive tract is composed of potentially absorbing cells, corresponding in function to the small intestine of higher forms.

The sluggish reptiles as a class have a definite large intestine marked off from the small intestine that joins the stomach. At the junction between the small and large intestines a new diverticulum, the *colic caecum*, appears (Fig. 215). The colic caecum of a turtle is hardly more than a slight enlargement, but higher up among rabbits and some other rodents it may become an enormously enlarged tube with an internal capacity nearly equal to that of the rest of the digestive canal to which it is attached.

Birds, which have evolved a long way from their reptilian forebears, have a much coiled small intestine, two colic caeca, and a large intestine

that is decidedly foreshortened, since it is incompatible with their strenuous aerial life to carry about the ballast of unnecessarily retained feces. The colic caeca are short in pigeons and comparatively long in owls and turkeys. In ostriches they are sometimes reduced to a single caecum, which is as capacious as all the rest of the small intestine and is made even more effective by the presence of a spiral valve.

The small intestine of mammals is usually easily distinguishable from the large intestine, a single colic caecum marking the transition from one region to the other. Exceptions are *Trichechus*, *Hyrax*, and the edentates *Dasypus* and *Myrmecophaga*, which have two colic caeca. Monotremes, flesh-eating marsupials, most edentates, insectivores, bats, carnivores, and toothed whales, either lack or have only a small colic caecum, but in herbivores it is so large that it may even exceed the body in length. Herbivores also have a noticeably longer intestine than carnivores.

The degenerate free end of the colic caecum forms the *processus vermiformis* in certain rodents, civets, monkeys, and man (Fig. 216). According to Wiedersheim the *processus vermiformis*, or *vermiform appendix*, in man, which has outlived its usefulness and bears an unsavory reputation, varies in length from two to twenty-five centimeters, with an average of about eight and one half centimeters. It tends to shorten with age and to become closed in later life. Statistics on the closure in 1005 observed cases are given by Müller in percentages as shown in Table IV.

TABLE IV. Closure of Human Vermiform Appendix

Age (in years)	Closure (Per cent)	
	♂	♀
1 to 10.....	2.0.....	0.0
11 " 20.....	5.1.....	5.4
21 " 30.....	6.4.....	8.7
31 " 40.....	12.7.....	23.8
41 " 50.....	26.2.....	34.8
51 " 60.....	20.5.....	30.0
61 " 70.....	29.3.....	50.0
71 " 80.....	38.7.....	26.0
81 " 90.....	53.3.....	52.0

The small intestine is divided more or less arbitrarily into *duodenum*, *jejunum*, and *ileum*, a distinction which, though first made out in man, applies to most other mammals.

The *duodenum*, or part next to the stomach, is comparatively short. The *jejunum*, which follows, and the more posteriorly located *ileum*, forming

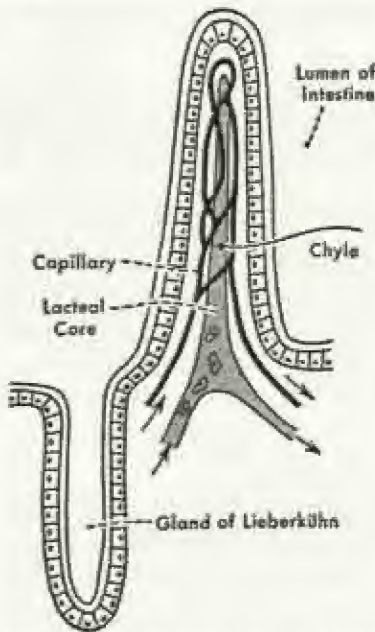


Fig. 260. Diagram of a villus and a gland, or crypt, of Lieberkühn.

about equal lengths of the remainder of the small intestine, are not distinctly marked off. The jejunum is richer in blood vessels as well as having a somewhat thicker wall and wider lumen than the ileum.

The characteristic modification of the lining of the mammalian small intestine is the presence of innumerable tiny thickset velvety projections, or *villi*, which enormously increase, in a minimum of space, the absorbing surface exposed to the dissolved food. In fact these are the definite organs of absorption.

Each villus consists of a thimble-like projection whose thin wall of cells encloses a capillary loop and a microscopic *lacteal*, or terminal element of the intestinal lymphatics (Fig. 260).

Fat that has been reduced to lower terms in the intestine passes into the lacteals and thence to the lymphatics, eventually emptying into the venous system by way of the thoracic duct. Digested proteins and carbohydrates are collected by the venous capillaries of the villi and carried to the liver by way of the portal vein.

In the ileum particularly, the forest of microscopic villi is frequently interrupted by irregular bare patches from half an inch to three or four inches in extent, which show like worn places in the nap of a Brussels carpet. These "intestinal tonsils," or *Peyer's patches* (Fig. 261), are lymphoid in character. It is important to remember that in typhoid fever the chief lesions occur in these areas. Smaller lymph nodes are also interspersed among the villi.

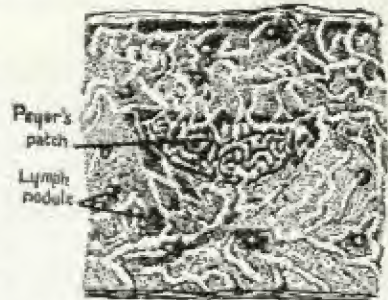


Fig. 261. Surface view of a portion of the mucous membrane of the ileum, showing a Peyer's patch, and solitary lymph nodes. (After Piersol.)

2. Glands

Two conspicuous glands differing greatly in appearance, intimate structure, and function, but which are alike in being endodermal derivatives of

the mesodacum, are connected with the duodenum just posterior to the pylorus. These are the *liver* and the *pancreas*. They are so large that, although they arise from the lining of the small intestine, they push through to extend entirely outside the digestive tube itself and come to occupy space within the body cavity.

(a) **Liver.**—The liver is an older organ, both ontogenetically and phylogenetically, than the pancreas. It should not be confused with the so-called "liver" of starfishes, crabs, mollusks, or other invertebrates, since it is in no way either homologous with or analogous to these structures.

Contrary to the popular impression, the vertebrate liver is not primarily an organ of enzymatic digestion, although the *bile* which it provides aids materially in the digestive processes by the stimulative action of the *bile salts* upon the enzymes of the pancreatic juice, by the emulsifying action of these salts, and by furnishing a favorable alkaline medium without which the digestive enzymes produced by the pancreas fail to act. In the bile itself no enzymes are present.

The liver, which has been characterized as the "busiest port on the whole river of life," is so voluminous that in man it may easily contain one fifth of all the blood, while several times an hour the entire blood supply of the body passes through its myriad capillaries, undergoing there profound modifications by way of additions and subtractions of constituent substances in the blood. Thus it acts like a strainer of the blood, storing sugar-fuel (glycogen) and then restoring it to the circulation when the muscles need it; balancing the circulating food ration generally by withdrawing and restoring certain constituents; eliminating bacteria; turning poisons into harmless wastes; abstracting nitrogenous by-products from protein compounds to be disposed of through the kidneys; and by drenching the intestine with the indispensable alkaline bile. No wonder Dr. Woods Hutchinson said of the liver: "It is all together the most useful and desirable citizen, and withall a cheerful and even convivial one, mixing our drinks, putting the stick into our vitamin cocktails, and the sugar and cream into life's coffee."

The bile is a bitter alkaline fluid, about ninety per cent water, tinged with pigments from the wreckage of red blood corpuscles and containing salts, both organic and inorganic, besides waste materials of different kinds. It is formed continuously in the liver and is poured at food-taking intervals into the duodenum where it mingles with the food-mass upon the escape of the latter through the pylorus into the intestine. The bile, which may amount to a pint or a pint and a half daily, contributes materially to the excreta that pass out of the alimentary canal. When an excess of bile is produced it may temporarily be stored between periods of digestive activity, by backing up into the *gall bladder*, a reservoir-like enlargement of the bile

duct (Fig. 266). That part of the bile duct that drains the liver is called the *hepatic duct* as distinguished from the *cystic duct* that comes from the gall bladder (Fig. 262). Whenever these two ducts join to empty into the intestine the common bile duct thus formed is called the *ductus choledochus*, a name that has the same root as "melancholy" and "choleric," words descriptive of conditions for which the misunderstood liver has been held responsible by the popular mind in the past.



Fig. 262. Diagram of the liver ducts in the human adult. (After Bremer.)

The choledochal duct and the duct of the pancreas open together into the duodenum of the horse, dog, cat, ape, and man, but separately in the pig, ox, rabbit, and guinea pig.

The gall bladder, which seems to be an emergency device for animals that digest a considerable amount of fatty food, is absent in many plant-eaters. Its total absence, as well as the abnormal presence of two gall bladders, has been noted in man. Its normal capacity in man is about an ounce and a half.

"Gall stones," which are found in the gall bladder in about 6 to 12 per cent of autopsies, are concretions composed chiefly of cholesterol but usually including bile pigments and calcium salts. Gall stones containing limy deposits may be detected by the X-ray. If large they are comparatively harmless, but while small they may block the ducts, thus causing the bile to be resorbed and passed back by way of the lymphatics into the blood stream, a condition that results in jaundice. The cystic duct especially lends itself to such obstruction, since it is modified within by mucous folds forming the *Heisterian valve*, which makes blocking the passage-way easier than would be possible if the lumen were entirely open.

The liver is an adaptive space-filler, weighing about one fortieth of the total body weight, and consisting usually of two or more lobes. Its shape and size are conditioned first by the abundant blood vessels, nerves and ligaments, or connective tissue attachments; second, by the neighboring organs which crowd it; and third, by the confining walls of the body cavity. With every breath that expands the neighboring lungs, and because of the uneasy

peristalsis of the stomach and intestine pressing upon it, the flexible lobes of the liver are constantly slipping slightly over each other, changing meanwhile somewhat in shape in accommodation and adjustment to the varying conditions of available space.

In mammals the two larger lobes are separated by the *umbilical fissure*, as determined by the *round ligament* representing the atrophied remains of the umbilical vein. A large *portal fissure* marks the gateway for the blood vessels, ducts, and nerves that pass to and from the liver in adult life.

In histological structure the mammalian liver is made up of cords of glandular cells in close contact with capillaries (Fig. 263) and with an elaborate system of drainage ducts and an adequate nerve supply. The whole mass of cellular cords and capillaries is embedded and encapsuled in a supporting network of connective tissue.



Fig. 263. Termination of a bile duct between liver cells. (After Huxley.)

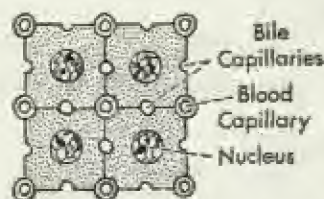


Fig. 264. Four adjacent liver cells, showing bile capillaries, or canaliculi. (After Jordan and Ferguson, and Merkel.)

Along the approximated sides of neighboring polyhedral gland cells that form the cords, are tiny intercellular spaces or grooves (Fig. 264), like the spaces between the fingers and knuckles when two fists are placed together. These *bile canaliculi*, formed as indenting intercellular grooves permeating the entire liver mass, empty into drainage ducts which compound with others in an ever enlarging array until they finally emerge as the single large outlet of the hepatic duct. The system of capillaries that enmeshes the gland cells is independent of the meshwork of canaliculi and drainage ducts.

The blood supply of the liver is unlike that of most other organs in that there are two sources from which it is derived, namely, the *hepatic artery* which brings blood from the heart in the same way as all organs of the body are supplied, and the *portal vein*, that comes freshly laden with dissolved food from the intestine. The capillaries derived from both of these sources hopelessly lose their identity as they gradually anastomose within the liver to form the *hepatic veins*, which drain the blood of the liver into the heart.

Embryonically the liver is a hollow ventral outgrowth near the beginning of the intestine just anterior to the attachment of the embryonic yolk sac (Fig. 265). It lies at first between two layers of ventral mesentery in the *transverse septum*, but eventually it becomes so large that it projects some

distance into the body cavity, pushing a covering of serosa, or visceral peritoneum, with it. The endodermal outgrowth from the gut itself becomes the secretory glandular part of the liver, and this soon becomes enmeshed with the vascular mesenchyme from the transverse septum and neighboring blood vessels, including the vitelline veins leading into the body from the yolk sac, to form the liver tissue. As the mass of this tissue grows into the transverse septum and the ventral mesentery, the material which is at the primary point of origin develops into the ducts and gall bladder.

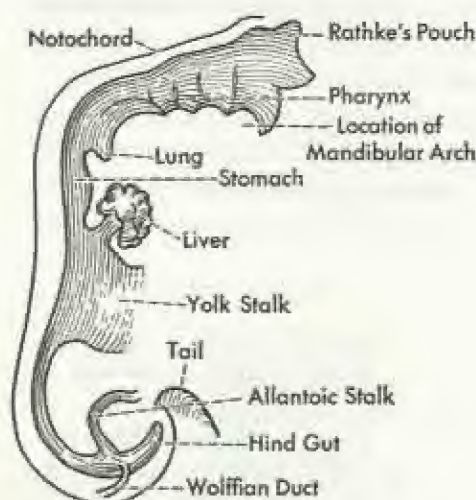


Fig. 265. Reconstruction of the alimentary canal of a 4.2 mm human embryo. (After His.)

forward (Fig. 13), that is beset with capillaries which bring food from the intestine, much as in the early embryonic phase of higher forms. It is lined with ciliated glandular epithelium and probably secretes a digestive fluid.

Typically the liver of most vertebrates has two lobes, although lampreys and snakes, perhaps on account of their elongated body form, have only one lobe. The liver is relatively larger in carnivores than in herbivores. In Anamnia, or fishes and amphibians, it is larger than in Amniota, or reptiles, birds, and mammals. This fact no doubt is connected with the presence of more fat in the diet of the former in each case. In certain carnivores, dogs and weasels for example, there are as many as seven lobes present.

In man four lobes are described (Fig. 266). The *right lobe* is the largest, constituting about four-fifths of the entire mass, while the wedge-shaped *left lobe* is next in size. These lobes are separated from one another by the *falciform ligament*. On the posterior aspect between these two major lobes, an oblong *quadrate lobe* lies near the gall bladder, while the small *caudate lobe* spreads between the *postcaval* and *portal fissures*.

In amphioxus the liver remains a simple, single sac projecting

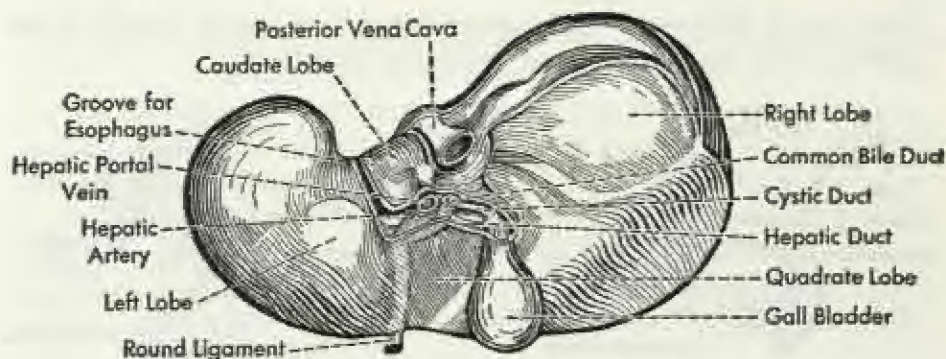


Fig. 266. Posterior surface of the human liver. (After Gray.)

(b) **Pancreas.**—The second largest vertebrate gland, the *pancreas*, is a compound alveolar gland of irregular shape lying in the fold between the stomach and the duodenum, and projecting into the body cavity from the point of its embryonic connection with the digestive tube, although in the lamprey, *Petromyzon*, and in certain teleosts, it may remain embedded in the wall of the intestine.

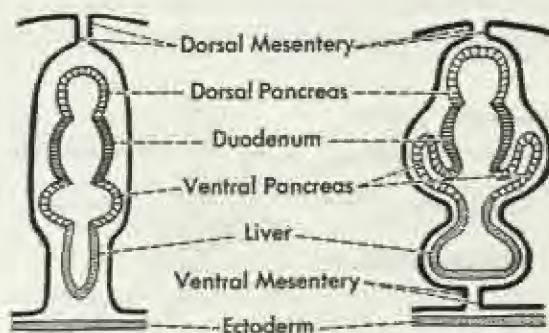


Fig. 267. Origin of pancreas and liver. (After Schimkewitsch.)

It arises as one or more endodermal outgrowths from the embryonic gut just posterior to the liver. These outgrowths are ordinarily three in number, of which one is dorsal and two are ventral in position (Fig. 267). The two ventral parts fuse together into a common gland, while the ducts formed at each point of outgrowth may either persist, or as is more often the case disappear with the exception of one (Fig. 268). The ducts of the ventral components are called *Wirsung's ducts*, while that of the dorsal pancreas is named the *duct of Santorini*. In some forms they unite either with each other to make a common duct, or with the bile duct. In lampreys all of the ducts are lost, the secretion of the pancreas consequently becoming entirely endo-

crine, that is, distributed by the blood rather than poured directly to the outside or into some passage-way leading to the outside.

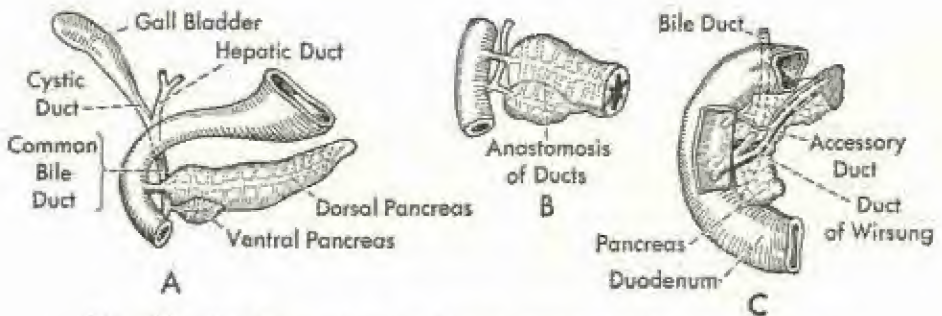


Fig. 268. Development of the human pancreas, showing origin from dorsal and ventral endodermal outpocketings. *a*, in 12 mm embryo; *b*, in 16 mm embryo; *c*, in child at birth. (After Arey.)

A curious modification of the pancreatic apparatus which not infrequently appears, particularly in the cat, is a *pancreatic bladder*, or reservoir-like enlargement of the pancreatic duct for the temporary storage of excessive secretion, an emergency organ quite comparable with the gall bladder that serves similarly as a storage reservoir for the bile of the liver (Fig. 269).

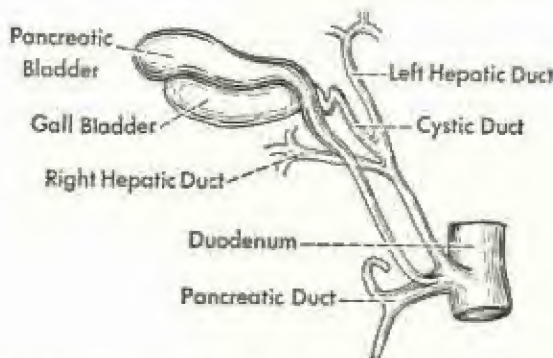


Fig. 269. Pancreatic bladder from a female cat. (After Boyden.)

In general it may be said that the pancreas is a gland of dual character since, in addition to its production of pancreatic "juice" which is poured into the intestine through ducts, there are present in the pancreatic tissue certain distinct interlobular cell aggregates, also endodermal in origin, called the *islands of Langerhans* (Fig. 270). These secrete substances (hormones) of a character quite different from the pancreatic juice itself, which are carried to all parts of the body through the circulating blood. The islands

of Langerhans vary from single interstitial cells to masses of several hundred. They are more abundant late in life than in youth, appearing in man when the human embryo is only about 54 mm. in length. It is estimated that in the pancreas of the guinea pig there may be present as many as 25,000 islands of Langerhans.

Which of these two kinds of secreting glandular cells, the endodermal outgrowths from the embryonic gut or the islands of Langerhans, represents the original pancreatic tissue, and whether one has or has not been derived from the other, is still a matter of controversy. It may be pointed out, however, that the islands of Langerhans are invariably present in all true vertebrates, and are undoubtedly early settlers if not the first inhabitants, whereas enzymatic secreting cells are wanting in certain vertebrates.

There is no pancreas in amphioxus. In sturgeons the pancreas is made up of two dorsal and two ventral components with only the right ventral *ductus Wirsungianus* remaining.

The pancreas of bony fishes and lower vertebrates generally is primitive in character, being widely diffused and irregular in form. Among mammals there is also a great variety in the form, position and size of this important gland. A single surviving embryonic pancreatic duct is found in man, Wirsung's duct, connecting with one of the ventral embryonic components.

The activating substance, or *hormone*, that is diverted from the islands of Langerhans into the blood has to do with the utilization of sugar in the tissues. Its failure to be produced in sufficient quantity results in diabetes, or the condition in which sugar is eliminated unused through the kidneys.

The substances secreted by the pancreas proper and eliminated through the ducts into the intestine are *enzymes*, which are essential in speeding up the chemical action begun in the intestine.

The principal enzymes in the pancreatic juice that aid in the digestive process are three, namely, *amylapsin*, which like the ptyalin of the saliva acts in making carbohydrates soluble; the inactive precursor of *trypsin*, which modifies proteins; and *steapsin*, which breaks down fats into simpler fatty acids and glycerine. These three important digestive enzymes, therefore, are prepared not only to transform chemically the three fundamental kinds of

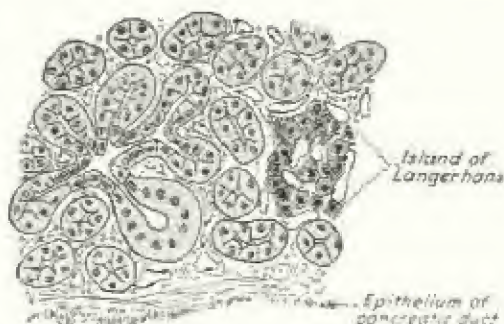


Fig. 270. Section through pancreas of rabbit. (After Krause.)

foods, carbohydrates, proteins, and fats, but also to render them fit for transference through the blood to all parts of the body.

In man about a pint and a half of digestive pancreatic juice is poured daily into the intestine.

(c) **Intestinal Glands.**—In addition to the liver and pancreas, the secretions of which are mixed with food materials in the duodenum, there are numerous smaller glands, occupying the walls of the intestinal tract, that likewise make chemical contributions essential to digestion. An intestinal juice that has been given the blanket name of *succus entericus* combines the products of these small, intestinal glands. Among mammals there are at least two kinds of intestinal glands that contribute to this juice, namely, *Brunner's glands* in the anterior end of the duodenum, and the *glands of Lieberkühn*, which are vastly more numerous, being embedded throughout the entire length of the small intestine in its walls. The multitudinous glands of Lieberkühn are in the form of sunken pits, or *crypts*, which are interspersed among the villi like deep gorges among steep mountains (Fig. 260).

Upon chemical stimulation by the *chyme*, which is the acidulated food mass that passes through the pylorus from the stomach into the duodenum, the epithelium of the small intestine produces a hormone called *pancreatic secretin*, which is carried by the blood to the pancreas where it excites that gland into activity. This reaction occurs only when chyme enters the intestine; otherwise, if continuously produced, the pancreatic juice much of the time would be wasted, not having any food upon which to act.

The *succus entericus* also includes several enzymes. *Enterokinase* converts the inactive *trypsinogen* of the pancreatic juice into the active *trypsin*. *Erepsin* completes the work of protein digestion begun by pepsin and trypsin. Other enzymes aid in carbohydrate digestion. Thus the intestinal contents include a variety of enzymes, derived from both pancreatic juice and *succus entericus*, which play a part in the complicated chemical preparation of the chyme for its transfer to the blood.

Most food material owing to its colloidal nature is inert and insoluble when taken into the digestive tract and cannot be directly transferred by osmosis to the circulating blood. Even water and inorganic soluble salts, that undergo no metabolic alteration in passing through the body, temporarily join hands with other substances in various combinations.

The army of *enzymes*, which are "substances of indefinite composition whose existence is known to us only by their action on other substances," play an indispensable rôle in making foods diffusible and available for use. Energy-producing carbohydrates, for example, if not taken in primarily in the form of soluble monosaccharids, must be made soluble by enzymatic

action. Such enzymes as ptyalin in saliva and amylopsin in the pancreatic juice change insoluble starches into soluble sugars.

The complex proteins have two fundamental uses, namely, production of energy and restoration of tissues. As with carbohydrates, proteins must first be reduced to soluble form by the action of enzymes before they can be oxidized to produce energy, while to restore worn-out tissues the diverse complex molecules that make up proteins must be broken down and reas-

TABLE V. Enzymes and Their Actions

TYPE	NAME	PLACE OF ACTION	RESULT
Amylolytic and inverting (Hydrolyzes starch)	Ptyalin	Saliva	Starch to maltose
	Amylopsin	Pancreatic juice	Starch to maltose
	Glycogenase	Liver and muscles	Glycogen to dextrose
	Invertase	Small intestine	Cane-sugar to dextrose
	Maltase	Saliva and small intestine	Maltose to dextrose
	Lactase	Small intestine	Lactose to dextrose and galactos
	Lactic acid fer- ment	Intestine	Glucose to lactic acid
Lipolytic (Fat splitting)	Steapsin	Pancreatic juice	Neutral fats to fatty acids and glycerines
	Lipase	Liver, etc.	Neutral fats to fatty acids and glycerines
Proteolytic (Protein splitting)	Pepsin	Gastric juice	Proteins to peptones and amino-acids
	Trypsin	Pancreatic juice	Proteins to peptones and amino-acids
	Erepsin	Small intestine	Proteoses to amino-acids
	Nuclease	Pancreas, spleen, thymus, etc.	Nucleic acid to purin bases
	Enterokinase	Small intestine	Trypsinogen to trypsin
Deaminizing	Guanase	Thymus, adrenals, pancreas	Guanin to xanthin
	Adenase	Spleen, pancreas, liver	Adenin to hypoxanthin
	Deaminase	Tissues	Amino-acids to oxyacids
	Arginase	Liver and spleen	Arginin to urea

sembled into the specific kind of molecules that are the building blocks which go to form the different body tissues. This process, like wrecking an old house to build a new one, calls for a succession of breaking-down operations, each dependent on a different enzyme.

In the disposition of insoluble fats two things happen: they are emulsified and then broken up into soluble fractions. Fats are said to be emulsified when mechanically broken up into particles of oil so small that each hangs suspended in a watery medium. Fats are chemically broken down into soluble fatty acids and glycerine, by such enzymes as steapsin in the pancreatic juice. These products are picked up by the epithelial cells of the intestinal lining in which they are reconverted into fats, which then pass into the lymphatic cores of the villi in emulsified condition, to arrive eventually in the blood stream. The emulsified fat, known as *chyle*, is milky in appearance as it is carried away by the lymphatics, which are therefore known as *lacteals* (*lact-*, milk). Of course milk itself is such an emulsion, too.

Enzymes and what they do, a subject so appalling to the layman, furnishes the happy hunting ground for the physiologist. A list of the principal enzymes concerned with digestion, prepared by Burton-Opitz, is shown in Table V.

VI. EGRESSIVE ZONE

The *large intestine* constitutes the egressive portion of the digestive tract through which the residue of the food mass is forwarded for expulsion after the usable part has been diverted through the walls of the small intestine into the circulating blood. Its diminished importance in the essential work of the digestive tract may account in part for the relative absence of structural modifications designed to increase its inner surface.

Except in the embryo it is without the villi which characterize the small intestine, and although Lieberkühn glands are present in lessening abundance along its lining, whatever glandular secretions are present are not so much concerned with chemical digestion as with mechanical lubrication of the feces from which the water content has been largely withdrawn.

The large intestine in man, which is about five feet in length, is differentiated into the *colon*, with *ascending*, *transverse* (from right to left), and *descending* portions, and finally the *rectum*, ending at the *anal opening* (Fig. 253). The colic caecum and the processus vermiformis, already mentioned, properly belong to the large intestine, although they occur at the junction between the small and the large intestine. The same parts characterize the large intestine of many mammals but are not so distinctive in

other vertebrates, since only the rectum of mammals is homologous with the large intestine of lower vertebrates. In the lower fishes as well as in the pipefish, *Syngnathus*, the stickleback, *Gasterosteus*, and others, the "large intestine" is actually smaller than the small intestine.

In man the colon, which is looped around the small intestine (Fig. 253), is characterized by three bands of longitudinal muscles, the *teniae coli*, that pull this part of the intestine together so as to form three rows of pouches, or *haustra*, along its entire length, a modification present in varying degree in the large intestine of other mammals. Attached to the external wall of the haustra there are also numerous small processes of connective tissue, often distended with fat, called the *glandulae epiploicae* (Fig. 218), but neither the haustra nor the glandulae epiploicae extend to the rectum.

In birds the rectal region of the large intestine is notably reduced. Since it is a disadvantage for these aerial creatures to carry about an unnecessary weight of useless fecal material, the provision for its temporary retention in a large intestine is curtailed, the excreta being disposed of as rapidly as assembled.

In many vertebrates, including monotremes among mammals, the urinary and genital ducts enter the posterior part of the large intestine, which thus receives not only the feces from the digestive tube but also the products of the excretory and reproductive organs. This region, the common exit for all three systems, is known as the *cloaca*. In most mammals the cloaca splits longitudinally during embryonic development, thereby separating the more ventral urinary and genital pathways from the more dorsal rectal portion concerned solely with the feces.

The rectum ends with the *anus*, which is kept closed by a sphincter muscle under the control of the will, unlike other circular muscles of the digestive tract that accomplish segmentation and peristalsis under involuntary control. The inner walls of the rectum in man are modified by two or three transverse crescentic shelflike folds, the *anal valves*, which are doubtless adaptations to erect posture, since they are absent in quadrupeds where the feces do not weigh against the anal sphincter.

Metchnikof, as well as others, has pointed out that the large intestine in man, particularly in the rectal region, is a danger zone, a veritable "sewage swamp," because bacteria of various kinds flourish upon the undigested residue of the food retained there, contaminating the body constantly with the fermentive and toxic by-products of their metabolism. In one tabulation of 1148 cases of cancer of the alimentary tract, eighty-nine per cent were located in the susceptible region of the rectum.

There are some obvious advantages to mankind in possessing a volumi-

nous large intestine and rectum where excreta may be held temporarily so that their evacuation may be timed and controlled more readily than in the case of flying birds, although the disadvantages are far from negligible. It is somewhat difficult to see how so unfortunate an evolutionary acquisition could have been fostered by natural selection, but the fact that it reaches its greatest elaboration in herbivorous animals, where it is still useful in caring for plant foods rich in cellulose, may give some hint of why such a danger zone came to be acquired and preserved in man.

VII. THE ESSENTIALS OF DIGESTION

A summary of the principal chemical adventures of food during its passage through the digestive tube is shown in Figure 271. The blood stream receives the food from the small intestine after it has been reduced to absorbable liquid form. This reduction, although partly mechanical, most of all involves a chemical breakdown into less complex substances, a process actuated by enzymes.

The irregular lines in the diagram indicate the particular glands from which each enzyme arises, and, at the wavy interval on the line, the general locality in the digestive tract where it is effective, and also the kind of food involved in each instance.

In conclusion it may be observed that when a hungry person sits down to a dinner table and surveys the viands spread before him, he rarely takes thought of all the necessary preliminary work that has made the occasion possible. Producers, handlers of raw materials, and an army of middlemen, as well as the manipulations of a cook, must at least be taken into account, yet in spite of all the detailed processes of preparation that have been involved, they are not a circumstance to what happens to the dinner in the twenty-five feet or so that it travels after it has been swallowed.

VIII. MESENTERIES

In the chapter on Embryology we have seen how the dorsal and ventral mesenteries are formed by the meeting of the hypomeres dorsal and ventral to the digestive tract. These mesenteries consist therefore of two layers of mesoderm continuous with the *parietal peritoneum*, lining the body cavity, and the *visceral peritoneum* (*serosa*), covering the digestive tract. Thus they serve both as attachments of the digestive tract to the body wall and as bridges for the passage of blood vessels and nerves, which run between the two otherwise closely applied layers. During embryonic development the mesenteries undergo many changes including the dropping out of most of the ventral mesentery and modifications due to the great elongation of the

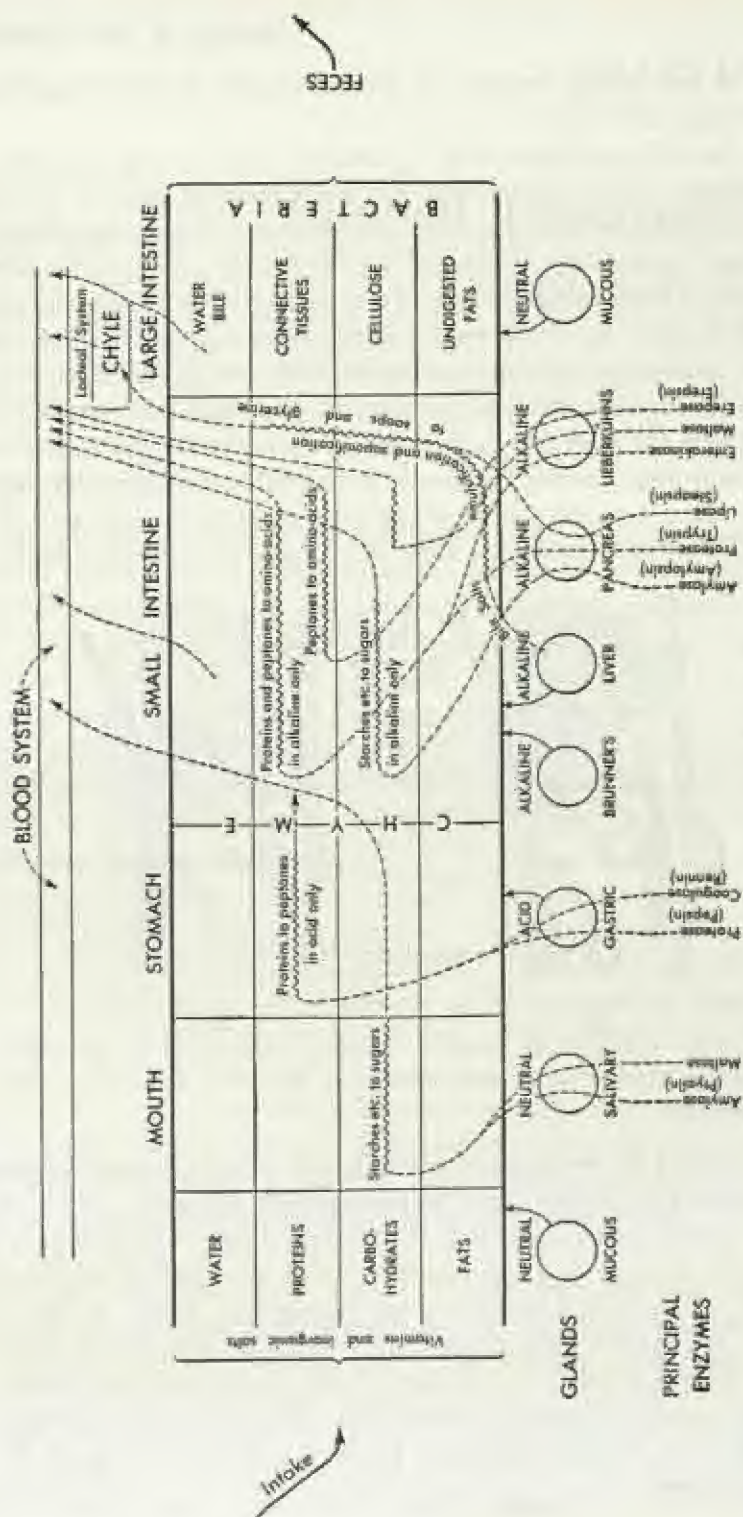


Fig. 271. The essentials of digestion.

intestine as well as the invasion of the mesenteries by such structures as liver, pancreas, and spleen.

With the differentiation of the abdominal digestive tract into stomach, small intestine, colon, and rectum, the corresponding parts of the dorsal mesentery become known as *mesogaster*, *mesentery proper*, *mesocolon*, and *mesorectum*, respectively. When the liver grows into the anterior remnant of the ventral mesentery, the part of the latter between liver and ventral body wall is called the *falciform ligament* (*ventral ligament of the liver*), while the part between the liver and the digestive tract is the *lesser omentum* in which run the bile duct, hepatic portal vein, and other smaller blood vessels. Where the liver has pushed the two mesenteric layers apart to lie between them they become the *serosa*, peritoneal covering, of this organ. A posterior remnant of the ventral mesentery also persists as the *ventral ligament of the bladder*, extending from that organ to the ventral body wall.

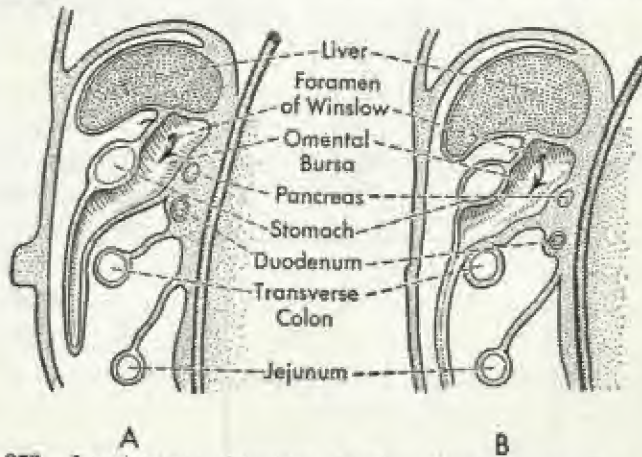


Fig. 272. Longitudinal diagrams showing development of the great omentum in man. A, at four months; B, in adult. (After Arey and Kollmann.)

In mammals the mesogaster, which it will be remembered is composed of two layers of peritoneal tissue, becomes greatly elongated until it extends from the stomach posteriorly, in between ventral body wall and the coils of the intestine, to serve as a sort of ventral protective blanket for the viscera (Fig. 272). This folded portion of the mesogaster, known as the *greater omentum*, is a bag the walls of which are two layers thick. Where these walls become closely applied to one another in the posterior part of the sac, this omentum is an apron four layers thick. The omentum is also a storage organ for extensive fat deposits, laid down between what were originally the two mesenteric layers.

Internal Transportation— Circulatory System

I. IN GENERAL

The circulatory system is the mechanism that attends to transportation within the organism of various substances needed for its sustenance.

Not only are food, water, and air taken into the animal body, but these indispensable substances must be distributed to every living cell wherever located, otherwise life would cease. Each living cell is a laboratory in which the chemical processes necessary for its existence are performed. Moreover, waste products, inevitable in the metabolic processes common to all living things, must be collected from every nook and cranny of the body for elimination, and transported either directly to the outside or indirectly by passages leading to the outside.

In microscopic unicellular animals internal transportation is accomplished by the movement of the cytoplasm within the cell itself. It is easy to see how small particles of food materials, once introduced into a protozoan like *Amoeba* for example, whose cell contents flow around like cold molasses, may shift their position within the cell body. This intracellular cytoplasmic movement, which is the simplest kind of a circulatory system, is entirely adequate for bodies of microscopic mass. It persists, moreover, as the final essential phase of circulation even in organisms built up of countless cellular units, since intake materials must not only reach each individual cell, but must also become incorporated and circulated therein as well.

In multicellular forms most of the component cells do not have direct surface exposure to the environment. The only way, therefore, that food, water, and air can enter the deeper cells of such organisms and penetrate to their ultimate parts, is either through or between the cells that form the body. The passing of materials *through* by osmosis from one cell to another is a slow and indirect method; also the ultimate cell in the series receives only what is left after all the intervening ones have taken their toll. Consequently it is a great improvement when passage-ways are opened up

between the cells so that materials may be forwarded freely, thus arriving at the ultimate cells directly and easily without repeated osmotic manipulation. The same sort of an advance in efficiency is seen when fire-fighters substitute a hose line for a makeshift hand-to-hand "bucket brigade." The circulatory system proper may be briefly described as consisting of a network of pipelines throughout the body, together with a fluid vehicle in the form of blood and lymph for transporting the various materials necessary for the life of the organism, and lastly, a mechanism for propelling these fluids through the channels of distribution.

II. BLOOD AND LYMPH—THE CARRIERS

1. Uses of the Blood

Mephistopheles, in Goethe's *Faust*, is biologically quite right when he exclaims: "*Blut ist ein ganz besonderer Saft!*" (Blood is a very peculiar fluid!)

In the first place it is not a lifeless fluid incapable of metabolic changes, but a *circulating tissue*, made up of detached living cells floating in a liquid plasma. The fact that it moves about marks it off distinctly from all other tissues. It is conspicuously kaleidoscopic in character, changing constantly in its intimate composition as it passes through the different parts of the body, for it is not only the common carrier to the various tissues of everything needful for their maintenance, but also the collector from the tissues of the products of metabolism, such as carbon dioxide and soluble nitrogen compounds.

In the last analysis cells of every kind within the animal body sooner or later contribute something to the blood and receive something in return, so that the blood reflects the entire metabolism of the body. In spite of this fact its component parts are normally kept at nearly a constant level. When serious deviations occur, as in the excessive loss of water from the blood during cholera, or the diminution of the number of blood cells in anaemia or hemorrhage, pathological consequences are sure to follow.

In general the following functions may be performed by the blood.

(a) **Equilibration of Water Content.**—Water is the fluid universal that facilitates the internal transport of materials, making good losses by evaporation and otherwise, as well as preventing the drying up of tissues. It is also the great solvent of all sorts of substances in the food and throughout the tissues. The degree of activity exhibited by any tissue is directly dependent upon the fluidity of the cytoplasm within its cellular units, which in turn is ultimately a matter of the amount of water supplied by the blood.

(b) **Liberation of Energy.**—Tissues “burn” in the presence of oxygen, thus releasing energy, which is what constitutes “living.” Certain softer tissues, like the muscles for example, lend themselves particularly to this oxidative process, while others, such as skeletal tissues, resemble more the iron girders of a “fire-proof” building, and do not burn as readily. The oxygen necessary for the release of stored energy is delivered to the tissues of vertebrates by the *haemoglobin* in the red corpuscles of the blood.

(c) **Distribution of Food.**—From one point of view blood is a solution or an emulsion of food substances carried in the plasma. To some extent also it transports food as solid undissolved particles engulfed in the white blood cells. It is thus the grocery delivery boy for the cellular community.

(d) **Regulation of Temperature.**—Body temperature, which results from the oxidation of the tissues, is equalized by means of the circulation of the blood, much as is the temperature of a building by the hot-water pipes of its heating plant. Such equalization is necessary because of the unequal production of heat-energy by different tissues of the body.

In so-called “warm-blooded” animals the body temperature is maintained at a practically constant level, regardless of the temperature of the environment, thus enhancing the animal's independence. “Cold-blooded” animals, on the other hand, owing partly to the low oxygen-carrying capacity of their blood, have a body temperature which fluctuates in response to that of the surroundings. A cold-blooded animal is consequently a thermal slave to the environment in which it finds itself.

It has been demonstrated, however, that even cold-blooded fishes when ill may show fever-like fluctuations in temperature.

(e) **Transmission of Chemical Substances.**—*Hormones*, the chemical messengers from endocrinal glands, frequently perform metabolic feats at some distance from their point of origin, after traveling along the blood highways. Drugs and poisons introduced into the organism likewise gain ready disposal over the body by means of the circulating blood. This is why a person with malaria, for example, feels “sick all over,” since the blood carrying the organisms producing malarial poison literally goes over the whole body.

(f) **Defense against Parasitic Invasion.**—Troublesome foreign invaders, such as infective bacteria and protozoans, are regularly combatted by white blood cells which capture and devour them. The cures of most “catching” diseases depend upon the successful outcome of this function of the blood.

(g) **Disposal of Cell Wreckage.**—The blood is a continual funeral cortege, in which are being borne away the “ashes” of dead cells, foreign bodies, bacterial products, and wastes of metabolism generally.

(h) **Chemical Elaboration.**—Furthermore, blood may be regarded as a peripatetic laboratory in which chemical transformations of wide variety are constantly going forward, as for example, the formation of "antibodies" of various sorts, oxidation and reduction of haemoglobin, elaboration of fibrin, and changes of fats and sugars to and from soluble states.

(i) **Clinical Diagnosis.**—All of the functions of the blood thus far indicated have to do with personal biological benefits to the animal itself. Blood may also be useful, outside of the individual who elaborates it, to the physician in identifying disease. No other tissue gives to the diagnostician so true a flashlight picture of the present state of the varying metabolism of the body as does the blood. The ease with which a sample of blood may be obtained for examination without injury to the patient, and the readiness with which deviations from the normal are revealed therein, have resulted in an increasing dependence upon it as a means of clinical diagnosis. For example, in a suspected case of either typhoid fever or appendicitis, the examination of the blood furnishes an immediate differential diagnosis, since in typhoid fever the number of white blood cells is below, while in appendicitis it is above normal. There is no doubt that dependence upon blood examination in future medical practice will increase as technic is further perfected and new approaches to the study of blood are developed.

2. Amount of Blood

In adult man the amount of blood is estimated to vary from about one twentieth to one fifteenth of the total body weight, that is from seven and a half to ten pounds for a person weighing one hundred and fifty pounds. This is approximately six quarts. In a new-born child the percentage of blood to body weight is less than in the adult, while in lower vertebrates the relative amount of blood is less than in mammals. Haempel gives the quantity of blood in fishes as less than two per cent of the total body weight.

The blood supply is temporarily increased in those regions that are active, as for example, in the wall of the stomach immediately after eating, or in that of the small intestine during digestion.

As to specific gravity, which is dependent mainly upon the amount of haemoglobin present, "blood is thicker than water." For man the figures have been given as 1.035 to 1.057 (with distilled water at 1.000).

3. Erythrocytes

Our sanguinary forebears, as well as our contemporaries, were well acquainted with the general appearance of blood, for the pages of history are copiously stained with it. Not until 1696, however, about two centuries

after Columbus had discovered America and his adventurous bones had turned to dust, did the Hollander, Anthony van Leeuwenhoek, find, with his primitive lenses, that blood is "composed of exceeding small particles." These he named *globules* which he said "in most animals are of a red color, swimming in a liquor, called by physicians the serum," and further, that "by means of these globules the motion of the blood becomes visible, which otherwise would not be discoverable by sight."

Red corpuscles are for the most part peculiar to vertebrates, although a few invertebrates, including the worms *Glycera* and *Phoronis*, the "blood clam" *Arca*, and the holothurian *Thyone*, also possess red blood cells. Ordinarily whenever invertebrates show red blood, as for example the pond snail *Planorbis*, the earthworm *Lumbricus*, or the larvae of the midge *Chironomus*, the haemoglobin producing the color is not located in red corpuscles but is dissolved in the plasma.

Red corpuscles, or *erythrocytes* as they are technically known, are directly concerned with respiration, the exchange of gases involved being facilitated by means of the respiratory pigment *haemoglobin*, which is present inside of the corpuscles. This pigment, which has a very complex molecule 68,000 times as heavy as the molecule of hydrogen, is a compound of iron and globulin, and possesses the ability to take on and give off oxygen readily. It is thus a sort of a shuttle device between outside oxygen and cells in the body that are in need of oxygen. Haemoglobin in the red blood cells is said to have the power of taking on seventy times as much oxygen as an equal volume of blood plasma, which can carry oxygen only in solution. The haemoglobin molecule thus loaded with oxygen assumes a brighter red color and becomes a very unstable substance, called oxyhaemoglobin. The peculiar ability of this molecular structure to transport the amount of oxygen necessary in breathing, may be destroyed by the action of certain "poison gases," such as carbon monoxide, for which haemoglobin has 250 times the affinity that it has for oxygen. When this gas, escaping from the exhaust of a running automobile engine in a closed garage, is inhaled, the oxygen of the oxyhaemoglobin molecule may be supplanted by carbon monoxide with the result that survival and recovery from suffocation will follow only if the person is hastily removed to fresh air where the oxygen will slowly replace the carbon monoxide. Haste is important to minimize the destruction of cells, particularly irreplaceable neurons. (See U. S. Pub. Health Bull. Vol. 195; 1930, No. 211.)

Erythrocytes of most vertebrates are oval discs that appear to bulge in the center on account of the presence of a nucleus. Among mammals (and lampreys!) erythrocytes are more circular in outline, with a single exception

in the case of camels and llamas which have oval erythrocytes resembling non-mammalian red blood cells in form. The nucleus in mammalian red blood cells disappears by extrusion, leaving the cell a degenerate sac, or *stroma capsule*, having an internal structure imperfectly understood but con-

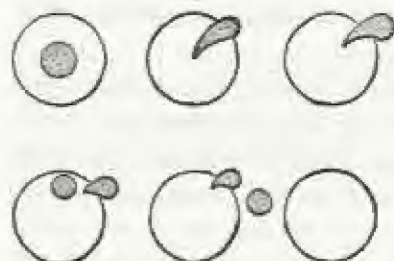


Fig. 273. Successive stages in the loss of a nucleus by an erythrocyte. (After Jordan and Ferguson.)

taining a concentrated solution of haemoglobin. The original name "corpuscle" (small body) fits the erythrocyte with more accuracy than "red blood cell," since nuclei are always associated with cells. Diagrams of the method of nuclear loss are shown in Fig. 273.

In size erythrocytes, measured from dried smears of blood, range from 75 micra (a micron is one one-thousandth of a millimeter) in the caudate *Amphiuma* to 2.5 micra in the musk deer *Tragulus*. Other measurements in micra for the longest diameter of blood corpuscles from dried smears have been reported as follows: *Proteus*, 58; frog, 22; turtle, 20; carp, 17; pigeon, 14; lamprey, 13; chick, 12; conger eel, 11; elephant, 9.4; MAN, 7.5; dog, 7.3; rabbit, 6.9; cat, 6.5; horse, 4.6; goat, 4.1.

In man the measurement is from 7.1 to 8.3, with an average of 7.5. In all these cases fresh corpuscles are slightly larger than dried smear specimens.

In general the smaller the corpuscles the more surface they expose for oxygen transfer in a given volume of blood, just as there is more "skin" in a bushel of small crab apples than in a bushel of big apples. One of the factors determining the "cold-bloodedness" of lower vertebrates as contrasted with mammals is the larger size of their erythrocytes with correspondingly smaller total surface of exposure for oxygen intake.

The number of erythrocytes in the blood is of considerable clinical importance. In man it is normally about 5,500,000 per cubic millimeter in the male and 5,000,000 for the somewhat less metabolic female, while in the highly metabolic infant the count is greater than in adults of either sex. The total number of red corpuscles in the average human being has been estimated at 30 trillions representing a respiratory surface 1500 times as large as the surface of the body itself. The number of erythrocytes varies with regard to the time when taken and other factors. According to Vierrodt the number of red blood cells of hibernating animals drops to as little as one third of the normal count during their "winter sleep." The red blood cells are more numerous during the day than at night and directly after eating or violent exercise, as well as in high altitudes when mountain climb-

ing or in airplane flights. Patients who are combating tuberculosis sometimes resort to high altitudes where the lessened pressure of rarified air is supposed to demand a greater surface exposure to haemoglobin to accomplish the normal amount of respiration, thus forcing the body to self-curative effort by producing more red blood corpuscles in compensation.

Haemolysis, that is the wearing out or destruction of erythrocytes, is the inevitable outcome of their strenuous travels through the blood channels. Physiologists have attempted to estimate the length of life of a single average erythrocyte by measuring the density of the pigments in the bile, since these are due principally to the haemoglobin released from the broken-down erythrocytes that are being eliminated. When capillaries of the skin are ruptured so that blood oozes out into the surrounding tissues, the liberated haemoglobin from the erythrocytes breaks down with a display of pigments, a good example of which is a "black eye" with all its rainbow-like variegations. The amount of haemoglobin necessary to produce a known degree of color in a measurable quantity of bile eliminated during a known interval of time, gives a rough idea of the rate at which new blood cells must be manufactured in order to maintain a comparatively constant level of erythrocytes throughout the entire body. Those who have ventured to speculate on this problem place the life span of a red blood corpuscle from ten to seventy days, which means that at the outside the erythrocyte population is completely renewed several times each year. Since the total number is estimated to be 30 trillion cells it means that the continuous production of red blood cells within the average human body, if reckoned on the most conservative basis, must go forward at the rate of *several thousand every second*.

The process of the formation of red blood cells, which is termed *haemopoiesis*, is accomplished before birth in the mesenchymatous tissues and also in the liver and spleen. In fishes and amphibians the spleen forms red cells even in the adult animal. In other adult vertebrates, particularly in mammals, haemopoietic tissue is mostly confined to the red marrow in the hollow bones, in which factory the major part of the astonishing output of erythrocytes takes place.

4. Leucocytes

Intermingled with red corpuscles in the blood are "white blood cells," or *leucocytes*, best described as wandering cells that are not always confined to the blood channels, and which are independent of the nervous system. Unlike the erythrocytes of mammals, these are detached cells that not only retain their nuclei throughout life, but also possess other characteristic features of true cells.

Within the same organism leucocytes show considerable differences with respect to the character of their nuclei, general size, shape, and function, differences that make possible their classification into three general categories, namely, lymphocytes, granulocytes, and monocytes. It should be noted that this classification is based on the leucocytes of human blood which have been most studied.

Lymphocytes (Fig. 274) constitute normally something like 22 to 25 per cent of all leucocytes. They are roughly spherical, with a single large nucleus, and are about the size of erythrocytes, being from 6 to 8 micra in diameter. No granules are present in their cytoplasm.

Monocytes are giant amoeboid mononuclear leucocytes, twelve or more micra in diameter, constituting normally from 2 to 10 per cent of all leucocytes. Their nuclei are relatively small while their abundant cytoplasm is without granules.

Granulocytes, which are somewhat larger than lymphocytes, being from 7 to 10 micra in diameter, are characteristically amoeboid in changing shape and are chemotactic in behavior. They are often referred to as "polymorphonuclear leucocytes" from the fact that their nuclei generally assume

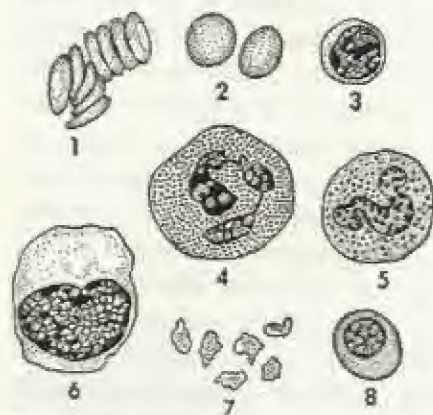


Fig. 274. Blood cells. 1, red blood corpuscles in *rouleau* formation; 2, red blood corpuscles, surface view; 3, lymphocyte; 4, polymorphonuclear leucocyte; 5, basophil leucocyte; 6, large mononuclear leucocyte; 7, blood platelets; 8, nucleated erythrocyte. (After Jordan and Ferguson.)

a variety of shapes. The granular cytoplasm, which gives the name "granulocyte" to these cells has differential staining properties that, according to Ehrlich, serve to classify them chemically still further into *neutrophils*, *eosinophils*, and *basophils*, depending upon whether the granules have an affinity for (*philos*, love) neutral, acid, or basic dyes, respectively. The two latter kinds are comparatively rare, forming only about 3 and 0.5 per cent respectively of the total number of leucocytes, while the neutrophils furnish in the neighborhood of 70 per cent. As these percentages vary within quite wide limits pathologically, they make an extremely valuable indicator of abnormal conditions for the clinician.

Dana and Carlson have pointed out that the number of new leucocytes contributed to the blood stream daily may be greater than the total average number present at any one time in the blood. In man the number of

leucocytes of all kinds varies from 2000 to 13,000 per cubic millimeter with a normal average of around 7000. The numerical variation is proportionately much greater than that of erythrocytes. There is a normal increase in the total number of leucocytes for instance after vigorous exercise or eating, upon exposure to cold, in infections, and during pregnancy. When the number rises over 10,000, a pathological condition is indicated.

With regard to their *origin* different kinds of leucocytes, like erythrocytes, may be produced in different parts of the body. In mammals certain embryonic cells in the marrow, *haemoblasts*, that do not circulate within the blood stream, are no doubt the busiest agencies for the manufacture of granulocytes as well as of red blood cells. Lymphocytes and monocytes are formed in lymphoid tissue throughout the body, in the *lymph nodes* and *lymph "glands,"* of which the spleen is the largest representative.

The three different kinds of leucocytes accomplish a variety of functions. For example, the wandering granulocytic neutrophils, as well as monocytes, remove worn-out tissue cells and invading bacteria by engulfing and digesting them in true amoeboid fashion, when they are known as *phagocytes* (*phag*, eat).

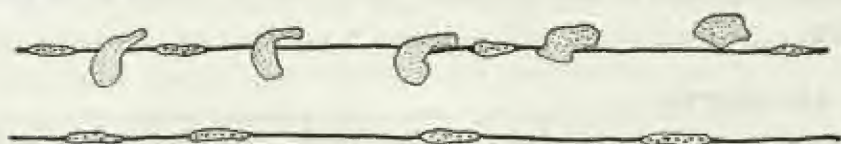


Fig. 275. Diapedesis, the passage of a leucocyte through the wall of a capillary. (After Clark, Clark and Rex.)

Owing to their amoeboid facility in assuming a variety of shapes they are able to squeeze between even the irregular edge-to-edge margins of the flat endothelial cells forming the thin walls of the capillaries (Fig. 275), thus escaping entirely from the closed blood system into the interstices between the cells of tissues everywhere in their phagocytic forays. This escape of the phagocytes through the capillary walls is termed *diapedesis*. There is indeed hardly a nook or cranny within the body that cannot be sought out and penetrated by these nomadic benefactors in the course of their sanitary and curative peregrinations.

The mobilizing of phagocytes is particularly well demonstrated when a wound becomes infected by bacteria. The "inflammation" that results in swelling and pain is due to the crowded ranks of phagocytes assembled for a battle royal with the invading army of bacteria. If the bacteria win, "blood poisoning" with its gruesome consequences results. If the phagocytes win,

health is restored. "Pus" is largely made up of dead phagocytes that have fallen in battle. Inflammation of the mucous membranes, or "catarrh," does not result in pus formation ordinarily, but in the production of a local excess of lymphatic fluid.

The holes in the capillary walls through which the phagocytes escape are immediately closed, like a puncture in an automobile tire, so that the red blood cells are kept within the blood vessels. Vagrant phagocytes, however, like the prodigal son, return to the blood stream. They do not reënter the capillaries from which they have escaped but are picked up by the lymphatic vessels that permeate everywhere between the cells of the tissues. By means of a system of valves these lymph-containing vessels forward their cargo by one-way traffic towards veins that enter the heart, and thus restore the runaway phagocytes to the general circulation.

Lymphocytes are neither amoeboid nor phagocytic, but monocytes and granulocytic neutrophils are both. Moreover, the non-phagocytic lymphocytes retain their spherical contour, never by diapedesis joining the phagocytes as "free lances of our corporeal militia" (Slosson). Instead they collect in the villi of the small intestine to engage in the transfer of fat globules, enmeshed in their cytoplasm, by way of the lacteals to the blood stream.

5. Thrombocytes

In addition to erythrocytes and leucocytes there are present in the vertebrate blood less well-known bodies, generally called thrombocytes.

In the frog these have been described as "spindle cells," intermediate in character between red and white blood cells, and able possibly upon occasion to be transformed into either.

Although true spindle cells with nuclei have been found in the blood of certain fishes, amphibians, reptiles and birds, they are not present in mammalian blood, their place being taken apparently by small bodies which Bizzozzero has named *blood platelets* (Fig. 274).

The unstable character of the thrombocytes is shown by the fact that they tend to mass together and disintegrate as soon as the blood is shed and exposed to air, which makes careful detailed observation of them difficult.

The term "thrombocyte" (*thrombus*, clot; *cyte*, cell) is not a very happy one to apply to blood platelets since it is doubtful if they are true cells but more likely small enucleated fragments of cells, with slight amoeboid motility. They have to do, however, with forming the "thrombus," or clot, that prevents excessive hemorrhage in case of wounds.

The different kinds of thrombocytes in human blood vary in size from

0.5 to 4 micra in diameter, thus being considerably smaller than erythrocytes. They have been estimated to number from 200,000 to 778,000 per cubic millimeter, with 500,000 given by Howell as an average for human blood. According to Wright blood platelets have their origin as fragments of the giant cells of bone marrow from which they are constricted off.

6. Plasma

Two thirds of the blood is fluid plasma in which the different kinds of cellular elements are borne along through blood vessels.

Plasma is about 90 per cent water, 9 per cent organic substances such as fibrinogen, paraglobulin, and serum albumin, and about one per cent organic salts, which brings it up to approximately the same density as sea water. Animals with blood of balanced density living submerged in sea water do not suffer from upsetting osmotic exchange, which can be dangerous or even fatal when it occurs suddenly as in the case of salt-water fishes that are transferred to fresh water or *vice versa*. The salts dissolved in human blood plasma are reminiscent of osmotic conditions long ago when our remote ancestors had not yet emerged from an aquatic habitat.

The plasma is a non-living fluid of much more chemical complexity than appears in the test tube. It contains a constantly changing variety of substances in solution, chief among which are dissolved food materials on the way to cellular delivery, and waste products that are being collected for elimination. There are also present *enzymes* of divers sorts which activate chemical changes: *opsonins*, that prepare trespassing bacteria for phagocytosis; *hormones*, the chemical messengers from endocrine glands on their way to the performance of tasks of internal regulation; *antibodies* and other problematical substances engaged in constant warfare against harmful invasion; and finally, *fibrinogen*, which although ordinarily free-flowing like other dissolved substances, can be turned when necessary into insoluble *fibrin*, that forms an entangling mesh like a barbed wire barrier through which cells do not easily pass. This is the *clot* which acts as an emergency plug to prevent the escape of blood from wounds while organic repairs are being made.

According to Howell, a substance in the plasma known as *prothrombin*, together with calcium salts, may form *thrombin* upon exposure to a rough or ragged surface, such as the edges of a wound that are unlike the smooth inner walls of blood vessels. Thrombin has the power of transforming soluble fibrinogen into insoluble fibrin which in turn entangles the blood cells and forms a clot.

Sometimes a blood clot forms around a solid body or breaks free from

a wound, when it becomes an *embolus*. Such a clot circulating within blood vessels may obstruct a capillary or a larger vessel and cause trouble. For example, if it blocks the first branching of the lung artery, it holds up the entire circulation and may cause sudden death. An embolus may arise from other causes than an outside wound, as in the case of "hardening of the arteries," when the wall of the blood vessel may become ruptured. If a traveling embolus is caught in the capillaries of the brain, it may give rise through pressure to a "shock," or apoplexy, recovery from which is dependent upon the removal or absorption of the embolus within a reasonable time.

If it were not for the mechanism of the blood clot, loss of blood from even slight wounds, or breaks in the walls of the blood vessels allowing leakage, would prove to be much more serious than it is.

Haemophilia is a hereditary condition in which some link in the chain that normally results in clot formation is missing so that the inability to stop blood leakage from even a small wound may result fatally. Persons thus afflicted are known as "bleeders." Males are more susceptible to haemophilia than females, since it requires inheritance of the trait from both sides of the house to make a female haemophilic, while inheritance through one parent is enough to cause a male bleeder.

III. BLOOD CHANNELS IN GENERAL

1. The Evolution of Organic Irrigation

Blood channels may be regarded as a device for increasing the inner surface area of an organism with reference to exposure to adequate nutritive and respiratory factors. In most invertebrates blood channels are largely open lacunar, or perivisceral spaces.

The first evolutionary stages in the development of a circulatory apparatus are perhaps to be seen in the porous sponges, whose "blood," that is, the surrounding water, carries a random load of microscopic food and dissolved air past the loosely organized colonial cells within the sponge body.

In flatworms, and some medusae also, there are neither true blood channels nor any specialized food-carrying medium of blood, since in these lowly creatures the digestive tube itself branches out like the twigs of a tree, extending between the cells of the body in such a way as to effect a direct delivery of needful nutriment without the mediation of a blood stream.

Among vertebrates two general types of channels appear, namely, a *haemal system of closed tubes* carrying blood, and an auxiliary *lymphatic*

system carrying lymph, which is practically blood without respiratory red corpuscles. In general these channels form an irrigation system of flexible plumbing, consisting of a continuous series of cavities, lined throughout with flat endothelial cells, in which the blood circulates.

The fact that blood is not subject to ebb and flow but is constantly in motion always in one direction, and that it repeatedly during life makes the entire circuit of the blood vessels, was established in 1619 by William Harvey (1578–1657), long before anyone actually saw the blood pass through the smaller connecting channels. It was Malpighi who in 1661 discovered the capillaries by which the out-going and in-coming blood vessels are connected. In 1696 Leeuwenhoek charmingly described the capillary circulation in a bat's wing as follows: "I perceived in many places an artery and a vein placed close beside each other and of a size large enough to admit the passage of ten or twelve globules at the same time; and in this artery the blood was protruded or driven forward with great swiftness, and flowed back through the vein, which was a most pleasing spectacle to behold."

Although the circulatory system penetrates to nearly every part of the living organism, there are a few regions of the highly differentiated vertebrate body that are not invaded by blood vessels of any kind, namely, the cornea of the eye, cartilage tissue, and the epidermis together with its derivatives, hair, nails, feathers, horns, claws, and the enamel of teeth.

2. General Plans of Circulation

Blood vessels are related to each other as shown in Figure 276.



Fig. 276. The relation of blood vessels to one another.

(a) **Annelid Plan.**—Two longitudinal blood vessels, one dorsal and one ventral, with collateral connections, and joined at either end by capillary networks, make up the main circulatory system of the practically heartless annelids. The blood flows forward through the dorsal vessel and backward through the ventral vessel in the simplest manner (Fig. 277).

(b) **Amphioxus Plan.**—The circulatory system of amphioxus is in many respects a preview of the basic vertebrate plan. In the first place the blood flows around in the opposite direction from that of the circuit in the annelid plan. By rotating an annelid 180° on its long axis, thus shifting its dorsal and ventral sides, the course of its general circulation may be brought into agreement with that of amphioxus.

As in the lower vertebrates, a large part of the anterior capillary system is associated with the pharynx region, which makes up about half the length of the digestive tube in amphioxus. Many of the posterior capillaries enwrap the remainder of the digestive tract. In addition there is introduced a new feature consisting of an extra capillary network spreading over the liver diverticulum to interrupt the vessel leading from the intestine to the gills. Thus an *hepatic portal system* is set off from the rest of the veins (Fig. 277).

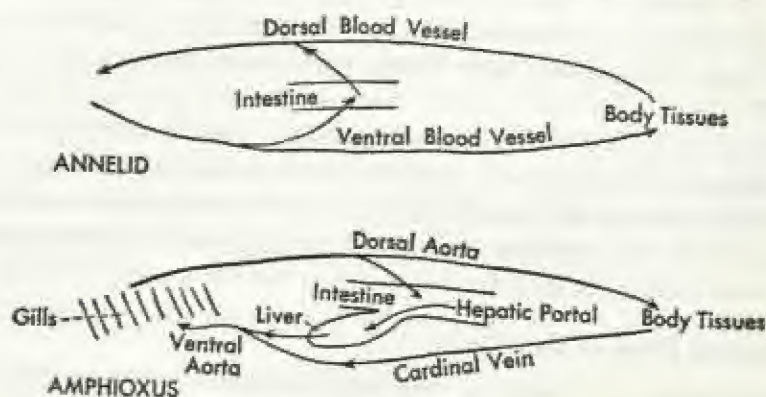


Fig. 277. Plan of circulation of annelid and amphioxus contrasted.

At the posterior end of the pharynx the *hepatic vein*, from the liver, is joined by *cardinal veins*, from the body wall, to form the *ventral aorta*, which carries blood to the pharyngeal wall. It is by means of peristaltic waves, which pass anteriorly along the ventral aorta, that the blood is pumped through the various parts of the circulatory system of amphioxus. At least the posterior part of this ventral aorta is probably homologous with the heart, the great pumping organ of vertebrates.

(c) **Gill Plan of Fishes.**—The amphioxus plan becomes further elaborated in fishes (Fig. 278) by the development of a heart, or blood pump, and by the introduction of an additional capillary complex involving the excretory organs, thereby establishing the *renal portal system*.

The heart is simply a muscular enlargement and modification of a part of the main ventral blood vessel, lying between the hepatic capillaries and

the gills, through which the blood flows forward. The development of the vertebrate heart from this *ventral* vessel has its possible homology in the rotated annelid plan, since in the latter it is the *dorsal* vessel which becomes muscular enough to pulsate and serve as a pumping organ.

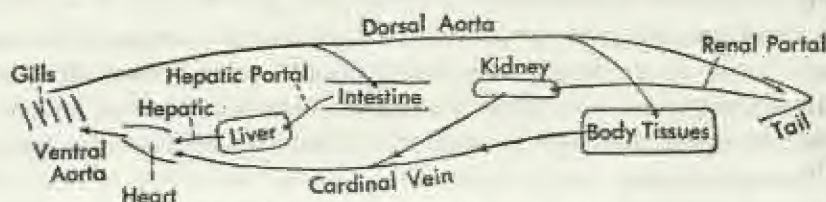


Fig. 278. Plan of circulation in a fish.

The return of blood from the region of the large propeller-like tail, characteristic of fishes, is effected by means of the renal portal system which carries the blood through a capillary network in the kidneys, whence it joins the main blood stream. In fishes, therefore, besides the capillaries which unite the outward-bound distributing system of blood vessels (arteries) with the inward-bound collecting system (veins), there are two major strainer-like complexes of capillaries within the kidneys and the liver respectively, that interrupt the large vessels and modify the stream of blood returning to the heart.

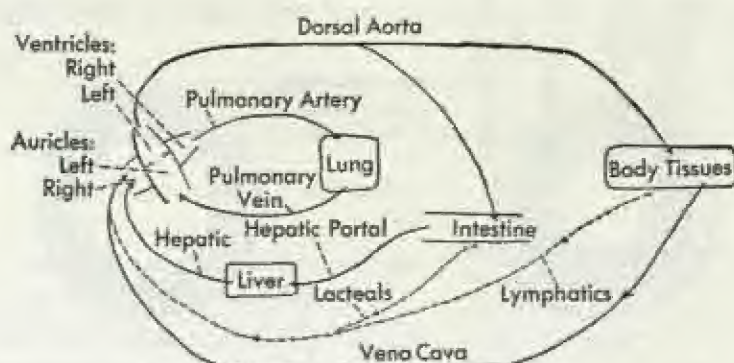


Fig. 279. Plan of circulation in a mammal.

(d) **Lung Plan of Mammals.**—The general plan of circulation among higher vertebrates, when reduced to the simplest terms, may be represented by a diagram (Fig. 279). The dotted lines, which are connected at only one end with the closed haemal circulatory system, show the relation of the auxiliary lymphatic vessels by means of which lymph is collected

from all regions of the body, together with the white blood cells that have escaped by diapedesis from the capillaries, returning them to the venous system just before reaching the heart.

The change from branchial respiration by means of gills to pulmonary respiration through lungs makes necessary the introduction of a double blood circuit, namely, the systemic circulation over the body and the pulmonary circuit to the lungs, with two central clearing houses, or hearts, instead of a single one as in fishes. These two hearts are placed so intimately together, however, that when looked at superficially they have the appearance of a single heart.

With the diminishing importance of the tail upon emergence from the water and the evolution of locomotion on land by means of legs, the renal portal system becomes discontinued. Thus it will be seen that the changing methods of respiration as well as of locomotion have modified the circulatory plan in land animals.

3. Structure of Blood Vessels

The walls of blood vessels show certain differences that serve to distinguish arteries, veins, capillaries, and lymphatics from each other.

Arteries and veins of the same size externally are not easily confused, since veins have thinner walls and a larger bore inside, and consequently are more liable to collapse than arteries when emptied of blood. The walls of both arteries and veins are made up of three layers of tissue (Fig. 280)

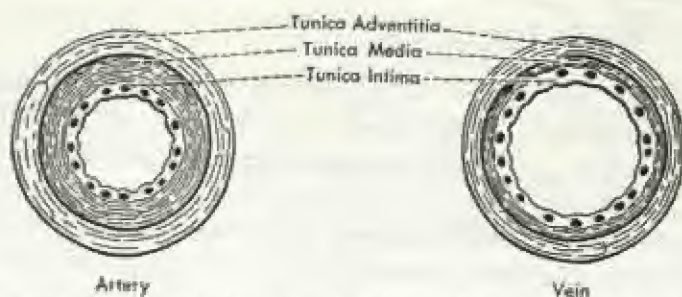


Fig. 280. Transverse section of an artery and a vein of corresponding size, showing the three layers. (After Huxley.)

known as *tunica intima*, *tunica media*, and *tunica adventitia*. The inside layer, or *tunica intima*, is invariably composed of a lining of flat endothelial cells, continuous and universal throughout all the blood vessels including the heart itself. This lining, except in the capillaries, is wrapped about by reinforcing connective tissue. The middle layer, or *tunica media*, is largely

composed of smooth muscle cells, arranged mostly in circular fashion and interspersed with connective tissue fibers, while the outer layer, or *tunica adventitia*, is principally connective tissue, more or less elastic and penetrated by lymphatics as well as vaso-motor nerve fibers that control the changing caliber of the blood vessel.

There are certain large veins in man, such as the umbilical, iliac, splenic, renal, and superior mesenteric, which are noteworthy because longitudinal muscle fibers also are found in the outside layer of the wall.

Arteries are thick-walled conduits carrying blood away from the heart, and are characterized by a well-developed elastic tunica media that is thick enough to maintain the shape of the blood vessel without collapse. The tunica adventitia in arteries is relatively thin.

As arteries follow their course throughout the body away from the heart, they gradually decrease in size, at various stages being called *arterioles* and *arterial capillaries*, until eventually they become *true capillaries* with very thin walls and minute bore, making it necessary for blood cells to pass in "Indian file" and even to assume distorted shapes in order to squeeze through.

The true capillaries, which lack both a tunica media and a tunica adventitia, form innumerable anastomoses and networks between the arterial capillaries on the one hand and the venous capillaries on the other. Arterial and venous capillaries, therefore, are transitional in location as well as in size and in thickness of their walls between the capillaries proper and arterioles and venules respectively.

Veins, which always take their rise from capillaries, are relatively thin-walled and collapsible. Since their walls are largely deficient in elastic tissue and muscle cells of the tunica media, the tunica adventitia becomes the most highly developed of the three layers in the walls of veins.

Pocket-like valves that prevent or hinder the back-flow of the blood (Fig. 281) are present in the larger veins but not in arteries, except in the immediate neighborhood of the heart of some gill-breathers. Valves are not present in all veins, being largely absent from the veins of the brain, cord, meninges, bones, and the umbilical vein, as well as most visceral veins, excepting branches of the hepatic portal system. The thin-walled veins are much more likely to anasto-

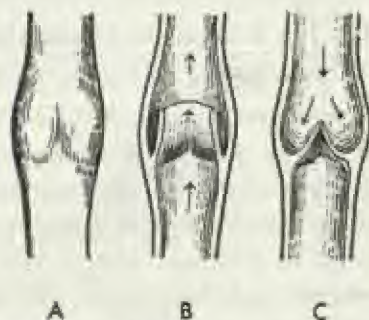


Fig. 281. Valves in veins. A, swollen vein from the outside indicating the presence of a valve; B, valve open allowing the blood to flow in the direction of the arrows; C, valve closed preventing the backflow of blood in the direction of the arrows.

more, become varicose, or to enlarge into sinuses, than the thick-walled arteries.

Lymphatics are typically varicose as well as capable of great distension. Ordinarily they do not acquire thick muscular or elastic walls and are very collapsible, although the larger lymphatics nearer the heart develop a definite tunica media with muscle cells that even enable them to pulsate. Lymphatics entwine around the other blood vessels in the most intimate fashion, yet do not communicate with them except at one or two definite openings near the heart where the lymph may be returned to the general blood stream. Lymph capillaries, although never as small as haemal capillaries, have the same sort of thin endothelial walls.

Physiologically, if not morphologically, the large serous cavities, such as the body cavity, and the pericardial and pleural cavities, as well as the synovial spaces around joints, belong to the lymphatic system, although their walls have a somewhat different origin and structure from those of ordinary lymphatic vessels.

Like veins, lymphatics possess valves along their course in the form of crescentic folds of the tunica intima which act like sluice-gates preventing the retreat of the fluid to any great extent in the direction away from the heart. Thus they establish one-way traffic in the lymphatic system.

4. The Rôle of the Capillaries

The first blood vessels to form in the embryo and the last to be discovered on account of their size are *capillaries* (*capilla*, little hair). Physiologically they are the most important part of the whole intricate system of blood channels in the vertebrate body, because in them the final transfers of the circulatory system are made. If the entire circulatory system be compared to a railroad system, the capillaries correspond to stations where passengers and freight are entrained and detrained, while the more conspicuous arteries and veins are simply lines of track connecting the stations.

Anatomists have always been more concerned with following out and homologizing veins and arteries, which it is possible to trace and describe, than with the nameless capillaries that defy isolation and cataloguing. When one considers Krogh's estimate that there may be at least 2000 capillaries permeating a cubic millimeter of human muscle, no one of which is over a millimeter in length, and that the total length of all the capillaries of the human body, if untangled and placed end to end, would be as much as 100,000 kilometers, that is, equal to two and a half times around the earth at the equator, it is small wonder that anatomists are forced to describe them in the most general terms.

Unlike the twigs of a tree that come to an end, capillaries are continuous and keep right on, forming anastomosing networks which have a larger total carrying capacity than the blood vessels they immediately connect (Fig. 282). The result is that the rate of flow of the blood stream slows down as it goes through the capillary networks, just as a swiftly flowing river that spreads out upon entering a lake loses its momentum. Blood cells in capillaries may be said to "crawl," but as the size of the blood vessels they are passing through enlarges, they "hustle" more and more.

In capillaries the rate of movement, which varies within wide limits, has been given as one twentieth of an inch per second, while in the highway of the aorta it is three hundred times as rapid.

Capillaries may measure from 0.003 mm. to 0.01 mm. in diameter, while the largest human arteries and veins sometimes attain a diameter of

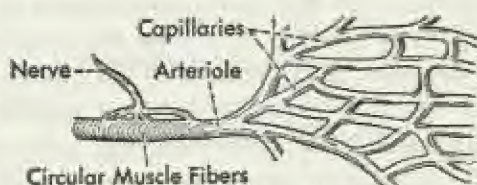


Fig. 282. A terminal arteriole, surrounded by a "stopcock" cuff of circular muscle fibers, which is supplied by a nerve ending for regulating the flow of the blood. The capillary network having greater internal expanse than the arteriole shows why the blood flows more slowly through the capillaries than in the arterioles. (After Keith.)



Fig. 283. Diagram to illustrate the behavior of red blood corpuscles in the capillaries. The arrows mark the course of the blood. *a*, a "saddlebag" corpuscle; *b*, corpuscle bending itself as it enters a side branch; *c*, deformity in a narrow capillary. (After Howell.)

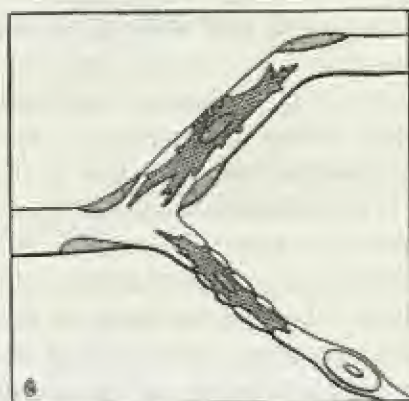


Fig. 284. Rouget muscle cells that control the caliber of the capillaries in the frog. (After Krogh.)

3 cm. This is a difference of 10,000 diameters or 100,000,000 times in carrying capacity. Single capillaries may be so small that, when undilated, blood cells that can penetrate a fine filter readily are unable to pass through

even in single file, or can only squeeze through with difficulty by temporarily distorting their shape (Fig. 283).

Although capillaries generally are intermediaries between veins and arteries, they may sometimes connect veins and veins, when they constitute a "portal system," or arteries and arteries, as in the "red gland" within the swim bladder of fishes, or in the glomeruli of the kidneys.

Outside the single layer of endothelial cells that form the walls of capillaries some vertebrates, but probably not mammals, have at intervals flat branching involuntary muscle cells (*Rouget cells*) that control the caliber of these minute vessels (Fig. 284). Resistance to blood flow is furthermore exerted by cufflike circular muscles around the arterioles and arterial capillaries under the control of *vasomotor nerves*. When the bore of the arteriole is lessened by the contraction of these circular muscles, blood cells pass into the capillaries at a slower rate or are temporarily excluded. The operation of these neuromuscular stopcocks of the arterioles is also influenced by mental states as reflected when a person is "pale with anger" or "flushed with joy."

IV. ORIGIN OF CIRCULATORY SYSTEMS

The beginnings of the circulatory apparatus appear very early, since the transport of food stuffs to the region where the new animal is destined to materialize is a primary necessity. In the chick the beginnings of the formation of the circulatory apparatus are as follows. As soon as the fertilized egg has undergone preliminary cleavage, and the potential pioneer cells have arranged themselves into the primary germ layers, certain marginal cells of the spreading splanchnic mesoderm become clumped together, forming so-called *blood islands* (Fig. 285). These consist of *haemopoietic* or blood-forming cells surrounded by flat endothelial elements which are destined to become the lining of future capillaries (Fig. 286). The blood islands thus form a halo around the embryo on the surface of the yolk between the endoderm and the splanchnic mesoderm. The developing capillaries that permeate the blood islands coalesce to form eventually a pair of definite blood vessels, the *vitelline veins*, one on either side. These lead directly into the growing body of the embryo where they unite into a common trunk which is the beginning of the future *heart* and *ventral aorta* (Fig. 287). Anteriorly the ventral aorta splits into two parts from which a pair of vessels, the *first aortic loops*, extends around onto the dorsal side of the primitive gut and leads into the paired *dorsal aortae*. The aortae communicate with *vitelline arteries* which emerge and continue outward to

the capillary field of the blood islands. This primary circuit, the first to be established in vertebrate embryos with well-developed yolk, is called the *vitelline circulation* and has to do with the transportation of food from the yolk sac into the body.

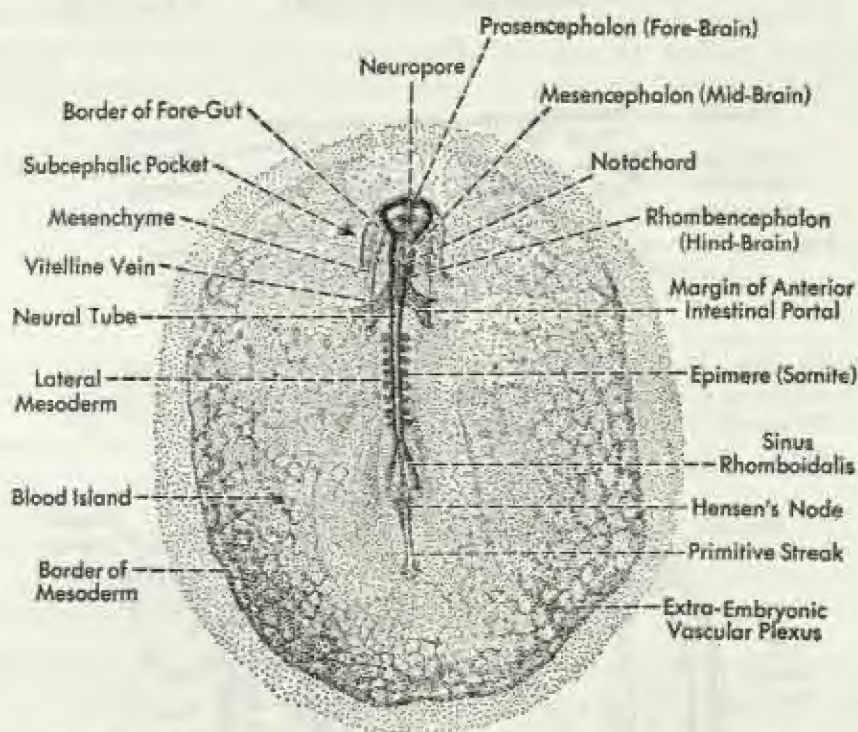


Fig. 285. Dorsal view of a chick embryo of about 28 hours. (From Patten, *Early Embryology of the Chick*, copyright 1929, by permission of P. Blakiston's Son and Company, publishers.)

Budding off from the vitelline circuit within the enlarging body of the embryo are secondary trunk lines which extend to and from both anterior and posterior regions of the body. These, together with relics salvaged from the temporary vitelline circuit, later make up the permanent *systemic circulation* (Fig. 288).

Still a third circulation, the *allantoic*, is temporarily necessary during the development of higher vertebrates to meet the conditions imposed by embryonic life within an amnion. It consists of a pair of *allantoic arteries* arising from the posterior region of the aorta, which extend out to supply the temporary saclike respiratory allantois. The returning *allantoic veins* enter the systemic circulation close to the entrance of the vitelline veins.

In mammals the allantoic arteries and veins become the *umbilical*

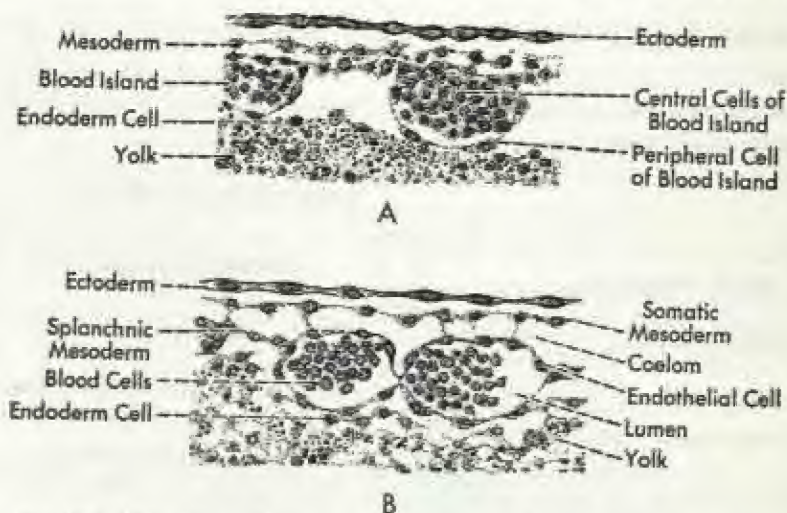


Fig. 286. Drawings of cross sections through the extraembryonic vascular area of a chick embryo, to show the organization of blood islands. (From Patten, *Early Embryology of the Chick*, copyright 1929, by permission of P. Blakiston's Son and Company, publishers.)

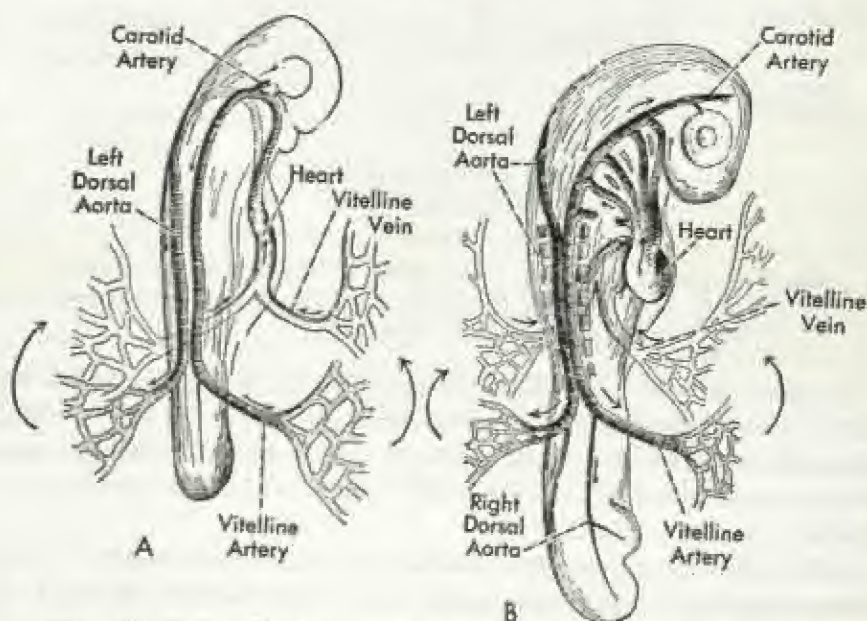


Fig. 287. Early circulation of vertebrate embryos. A, appearance of vitelline circulation; B, later stage, during formation of aortic arches. (From Wilder, *History of the Human Body*, copyright 1923, by permission of Henry Holt and Company, publishers.)

arteries and veins that form the respiratory bridge through the *placenta* between the fetus and mother. The placenta itself is a compound capillary mammalian organ of double derivation, the part from the allantois of the embryo interdigitating into the uterine wall of the mother so that by osmosis there can occur a transfer of materials between the blood of the two. In the earliest known human embryo in which the circulation is described, the allantoic component seems to take precedence over the vitelline circulation, a state of affairs not unexpected since in mammals, as contrasted with

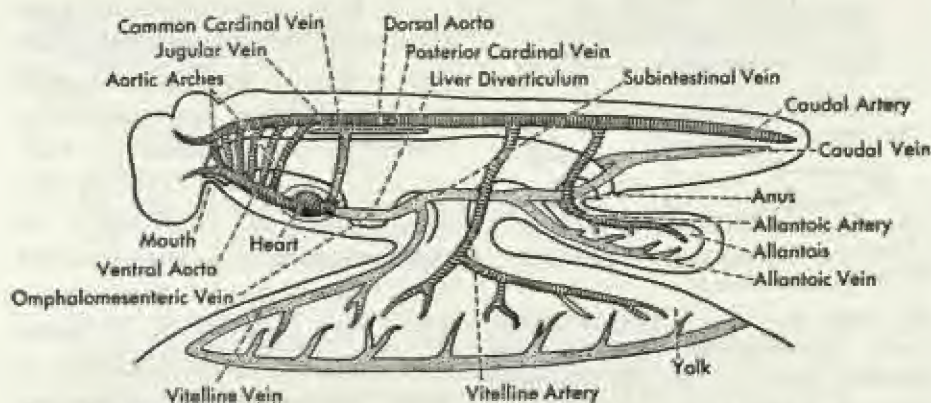


Fig. 288. Diagram of embryonic circulation in a large-yolked vertebrate. (After Kingsley.)

reptiles and birds, the yolk sac and the accompanying vitelline blood vessels play a rôle of ever decreasing importance. The need of a vitelline circuit wanes with the vanishing yolk, while the allantoic circuit becomes useless upon hatching or at birth. Thereafter the systemic circuit takes up its constant functions and maintains them throughout life. The precarious transition from embryonic to permanent circulatory devices involves profound modifications. In mammals, where the umbilical cord is severed at birth, it is very abrupt.

V. THE HEART

1. In General

The vertebrate heart, which is essentially a modified blood vessel half artery and half vein, consists of two kinds of chambers, a thin-walled venous *receiving chamber*, where the returning blood collects, and a thick-walled *arterial muscular forwarding chamber*, separated from the former by valves

which prevent the retreat of the blood when the muscular walls contract (Fig. 289).

The walls of the heart are composed of the three histological layers common to blood vessels, with the exception that the involuntary muscle

cells of the tunica media are of a peculiar striated branching type which is particularly effective for the enormous and unremitting work that the heart has to do.

Dr. Keen apostrophizes the heart as follows: "The heart is one of the most wonderful pieces of mechanism in the world, more powerful in proportion to its weight than any Baldwin locomotive, more delicately constructed than the finest watch, an organ which must do and—*mirabile dictu!*—does do its own repairs while busy at its work. It knows no Fourth of July or Christmas or Easter holiday, never can even know the joy and relief of sleep, 'tired

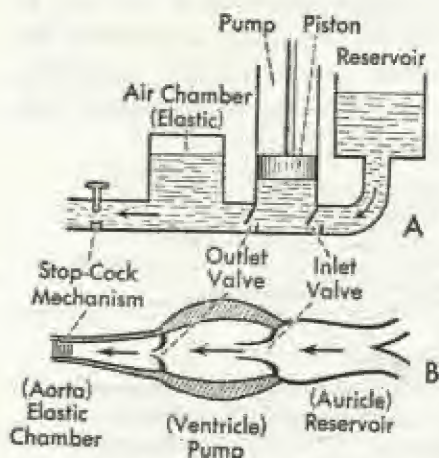


Fig. 289. The various parts of a force pump (A), compared with the corresponding parts of the left ventricular pump of the heart (B). (After Keith.)

nature's sweet restorer.' It begins its orderly reiterated contractions and relaxations long before birth, and they cease only at death. It must continue them in health and in sickness, when its function is often sadly disturbed. In mid career let it stop for but a few moments and death comes swiftly, almost instantly."

2. Embryonic Development

As the ventral parts of the hypomeres approach one another to form the ventral mesentery in the region of the pharynx, they thicken. Between them mesenchymal cells establish two thin-walled endothelial tubes (Fig. 290). These vessels soon fuse into a single *endocardial tube* surrounded by thickened ventral mesentery the layers of which meet both above and below the tube as *dorsal* and *ventral mesocardia*, respectively. While the *mesocardia* disappear almost immediately, the rest of the ventral mesentery, adjacent to the endocardial tube, continues to thicken, especially in the region where the ventricle is to form. The wall of the original endocardial tube becomes the *endocardium*, the lining layer of the adult heart, while the surrounding material develops into the *myocardium*, the muscular layer

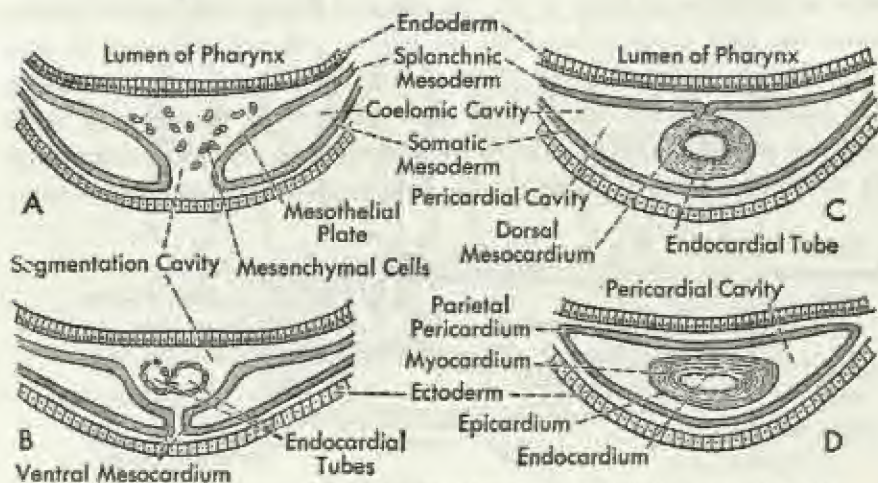


Fig. 290. Diagrammatic cross sections showing the formation of the heart. In A the descending mesothelial plates have nearly met, with a number of mesenchymal cells between them. In B the plates have met ventrally; most of the mesenchymal cells have been utilized in forming a pair of endocardial tubes. In C the endocardial tubes have united; the plates have met dorsally; the ventral mesocardium has disappeared; additional mesodermal cells are grouping about the single endocardial tube; and the pericardial cavity has been established. In D the dorsal mesocardium has disappeared, and the primordium of the heart is attached to the wall of the cavity only at each end, as in Figure 291a. Three layers of the cardiac wall are now evident, namely, the endocardium, the lining layer; the myocardium, or muscle layer; and the epicardium, or visceral pericardium, the covering layer.

of the heart, and a thin covering layer, the *visceral pericardium*. With the disappearance of the mesocardia, the heart lies free in the *pericardial cavity* attached only posteriorly, at the transverse septum, and anteriorly at its exit where it passes over into the ventral aorta (Fig. 291).

Although the heart is at first a relatively simple tube, it soon enlarges and becomes modified. Included among the changes which occur are: *constrictions* into several chambers; *differential thickening of the myocardium*, resulting in the establishment of the thin-walled receiving part and the thick-walled forwarding part of the heart; and a *linking* of the chambers, necessitated by rapid growth within crowded quarters, so that they no longer lie in a straight line.

3. Evolution

In amphioxus, in which the circulatory apparatus is so primitive that red blood corpuscles are scarce, an accessory lymphatic system is not yet

present and there is no heart at all. The ventral blood vessel which extends between the liver diverticulum and the gills is contractile enough to send the blood forward. It is this part of the ventral aorta that marks the location of the future vertebrate heart. From such a beginning the evolving vertebrate heart passes through a series of modifications of increasing complexity, until eventually there is developed the four-chambered mammalian heart.

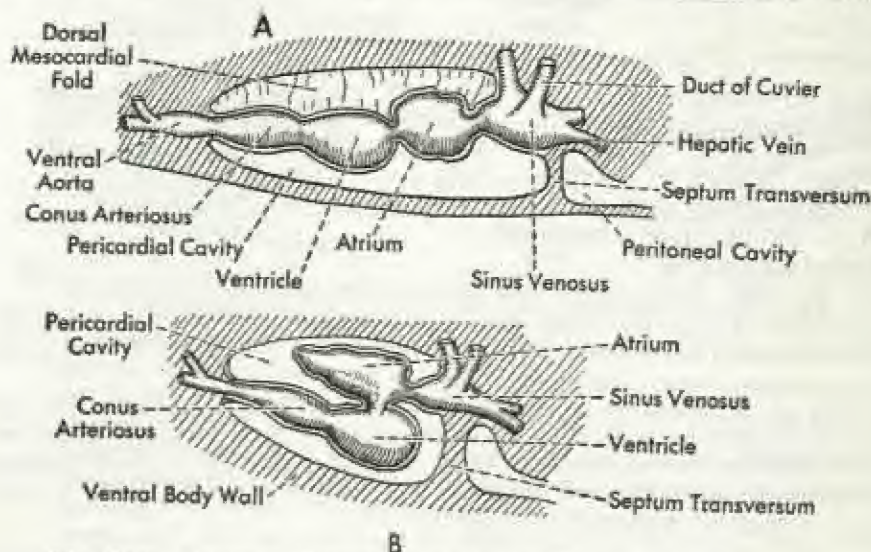


Fig. 291. Diagrams illustrating relation of heart chambers to one another and to pericardial cavity. A, hypothetical primitive condition; B, selachian stage. (After Goodrich.)

The first step in the differentiation of the vertebrate heart is encountered in the larval *ammocoetes* stage of the lamprey eel in which the prophetic ventral aorta lying between the liver and the gills becomes somewhat enlarged and modified by constrictions, unequal thickening, and kinking. Although the ammocoetes stage of the lamprey shows the heart still in the common body cavity with the liver, intestine, and other visceral organs, among fishes generally a *transverse septum* forms by a proliferation of the peritoneal walls, and ever after the heart is housed within the privacy of an enveloping space of its own, the *pericardial cavity*.

In elasmobranch fishes the *pericardio-peritoneal canal*, a slitlike opening between the pericardial cavity and the peritoneal cavity, represents the last step before the establishment of pericardial independence.

(a) **Single-circuit Hearts.**—The relatively small heart of fishes consists typically of a series of four chambers through which only non-aërated blood passes, since the spent blood sent forward from the heart to the gills for

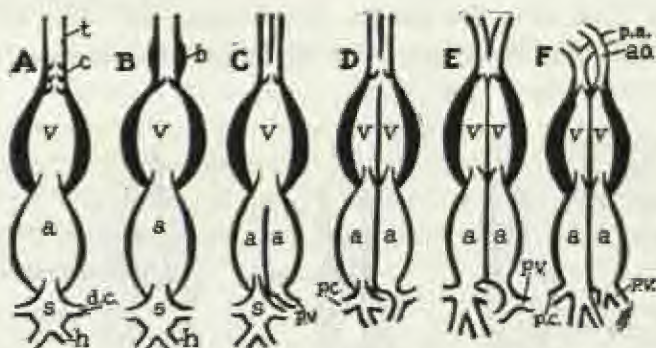


Fig. 292. Evolution of the heart. A, elasmobranchs; B, teleosts; C, amphibians; D, lower reptiles; E, alligators; F, birds and mammals; a, atrium or auricle; v, ventricle; a.o., aorta; b, bulbus arteriosus; c, conus; d.c., duct of Cuvier; h, hepatic veins; p.a., pulmonary artery; p.c., post-caval vein; p.v., pulmonary vein; s, sinus venosus; t, truncus arteriosus. (After Kingsley.)

aëration must make the grand tour of the body and become again non-aërated before it is returned to its starting point in the heart.

Beginning posteriorly the four chambers in the heart of elasmobranch fishes are the *sinus venosus*, *atrium*, *ventricle*, and *conus arteriosus* (Fig. 291B). The first two belong to the receiving region of the heart and are reservoirs with elastic rather than thick muscular walls, while the ventricle is thick-walled and muscular, as befits the forwarding pump of the blood. The conus has a muscular wall of moderate thickness, which by its elasticity aids in regulating the back pressure of the blood as it is forced through the *ventral aorta* into the nearby capillaries of the gills.

In elasmobranchs the single atrium receives the blood that has been poured into the sinus venosus from the ducts of Cuvier and the hepatic veins (Fig. 292). A row of cup-like valves, with their concavities in front, guard the *atrio-ventricular opening* permitting the blood to go into the ventricle but filling with blood to block the opening when the ventricle contracts to force the blood through the conus (Fig. 293). Several rows of *semilunar*

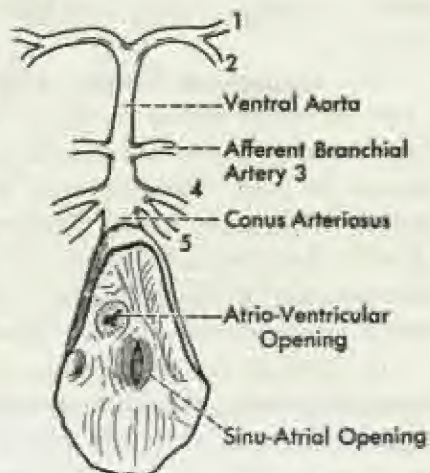


Fig. 293. Heart and ventral aorta of *Squalus acanthias*, from the dorsal side, with the atrium cut open. (After Röse.)

valves in the conus allow this blood to flow forward but, when the ventricle begins to relax, they block the conus by filling with blood as soon as it starts to flow backwards (Fig. 294A).

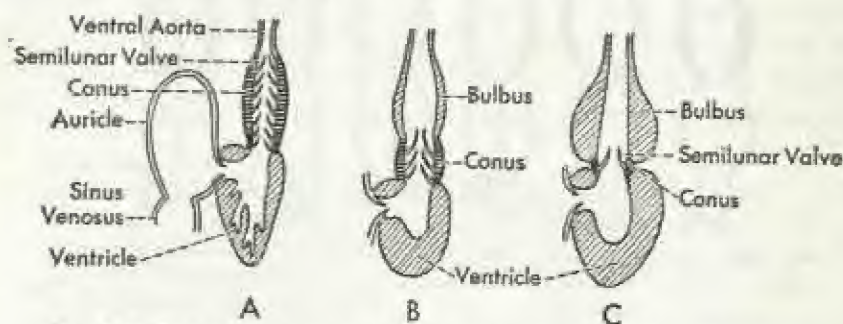


Fig. 294. Schematic long section through the hearts of various fishes to show the relation of the conus and bulbus. A, elasmobranch; B, ganoid; C, teleost. (After Boas.)

In bony fishes the conus and ventricle gradually telescope together until in most teleosts the conus is represented by a very short region including a single row of semilunar valves (Fig. 294). With this shortening, the posterior part of the ventral aorta is drawn back into the pericardial cavity where it develops a thick muscular wall and becomes known as the *bulbus arteriosus*.

(b) **Transitional Hearts.**—With the introduction of land life and lungs a new secondary shorter circuit is initiated by means of which aerated blood from the lungs is returned directly to the heart before making the excursion around the body. The pulmonary blood is poured into the left side of the atrium, a partition having developed that divides the original receiving chamber longitudinally into two chambers, a *right* and a *left auricle*. This *interauricular septum* develops to the left of the opening from the sinus which therefore sends all of its blood into the right auricle (Fig. 292c).

In dipnoans and amphibians, which accomplish the precarious transfer from gills to lungs, there is thus developed what may be regarded as a heart and a half, or a heart with one ventricle and two atria or auricles. The auricular partition is incomplete in dipnoans so that a mixture of aerated and non-aerated blood results within the auricles of the heart through the so-called *foramen ovale*. However, as this mixture is passed on through the ventricle, a twisted partition in the conus, which has not yet become incorporated in the ventricle, tends to shunt the mixed blood two ways, that is, to the lungs and over the body.

In amphibians while the auricular partition is complete and the foramen

ovale is obliterated, there is a mixture of aerated and non-aerated blood in the common cavity of the ventricle. When sent over the body without having first been revived by a trip to the source of oxygen in the lungs, there results a condition comparable with burning coal that is half burned-out ashes and "slag." It burns poorly. This is one reason why these animals are "cold-blooded," since the only pure blood in an amphibian is in the short pulmonary veins.

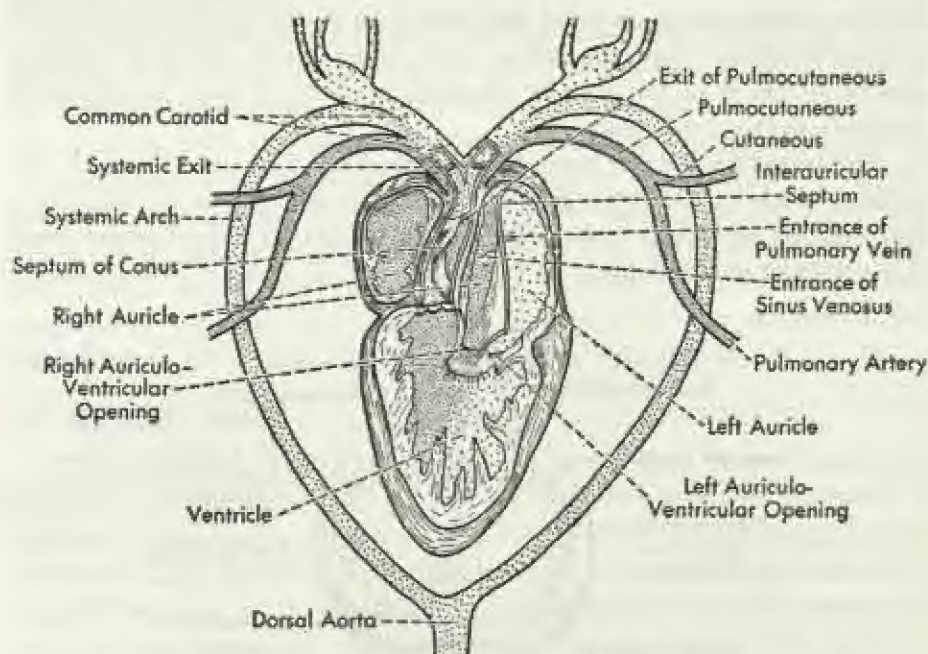


Fig. 295. The transitional heart of a frog showing the beginnings of differential distribution of blood despite the retention of a single ventricle. (Heart modified from Kerr.)

This handicap of mixed blood within the ventricle of the amphibian heart is partially avoided by the rapidity of the heart-beat which does not allow time for a thorough mixing of the two kinds of auricular blood that enter the ventricle from the two auricles, and by the spongy reticular structure of the ventricular chamber. Every time that the ventricle is filled, the mass of blood occupying the ventricular cavity may be thought of as momentarily of three kinds, arranged in a sort of temporary stratification, with non-aerated blood from the right auricle placed nearest the exit of the ventricle (Fig. 295), the aerated blood from the lungs farthest away from this exit, and the inevitable mixture of the two somewhere in between. As

the ventricle expels its contents before these relations have time or opportunity to change, the result is that the non-aërated blood nearest the exit is directed by the *septum of the conus* into the first possible avenues of escape, which are the *pulmonary arteries* leading to the lungs. The intermediate mixed blood, unable to enter the already filled arteries to the lungs, is forced along into the next available blood vessels, which are the *systemic aortae* distributing blood over the body generally. The best aërated blood of all at the bottom of the ventricle, being the last to emerge and finding all other passage-ways crowded full, passes on to the *carotid arteries* that supply the brain. Thus the brain, that always needs the best available aërated blood, is in the way of obtaining it, even in such unintellectual ancestors as frogs and toads.

The transition from a single to a double heart is further shown in the reptiles, which have come to forsake entirely the gill method of respiration, but, with the exception of the Crocodilia, have not yet arrived at the estate of a complete double heart.

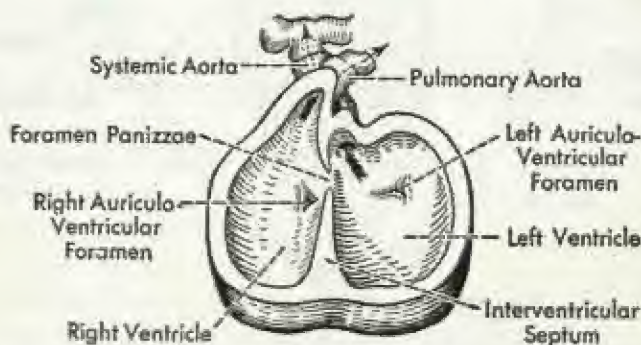


Fig. 296. Human heart of a 7.5 mm embryo, cut open. (After Kollmann.)

Among reptiles an *interventricular septum* forms which tends to keep separate the aërated blood, returning from the lungs by way of the left auricle to the left side of the ventricle, and the non-aërated blood of the body entering the right side from the right auricle (Fig. 292D). This partition is incomplete in most reptiles, so that there still exists some degree of mixture between the right and left ventricles through the *foramen Panizzæ* (Fig. 296), which represents the last gap in the uncompleted ventricular septum. Non-aërated blood from the right ventricle goes out not only to the lungs but in part also to the dorsal aorta, the main distributing trunk of the body. The result is that in reptiles, although the blood is kept unmixed as far as the dorsal aorta, from that point on it is mixed blood,

being distributed over the body with a corresponding inevitable sluggishness of behavior.

(c) **Double Hearts.**—In the Crocodilia (Fig. 292E) the foramen Panizae finally becomes obliterated and two complete hearts, superficially incorporated into one, are established. One of these hearts, made up of the left auricle and powerful left ventricle, constitutes the pump for the major circuit over the body, while the other, the right auricle and right ventricle, takes care of the blood coming back from the general body tissues and being sent to the lungs.

Aërated and non-aërated blood, which are mixed within the single ventricle of the heart in amphibians and in the dorsal aorta of reptiles, are kept completely separate among birds and mammals. As in Crocodilia the blood of birds and mammals passes alternately through two circuits, the pulmonary and the systemic. Blood entering the right auricle is sent into the right ventricle, then out to the lungs, back to the left auricle, to left ventricle, out to the general body tissues, and back once more to the right auricle. In birds and mammals the telescoping of the receiving chambers reaches the point where the sinus venosus is virtually eliminated, the chief systemic veins emptying directly into the right auricle.

4. Size and Position

The heart of a bird is proportionately larger than that of any other vertebrate, for the reason that an especially efficient pumping apparatus is required to keep the machinery of strenuous aerial locomotion going. Among mammals small species have relatively larger hearts than large forms. The proportionate size of the heart also decreases with the relative decrease of the heat-dispersing body surface that accompanies growth. For example, the weight of a newly-born rabbit's heart has been found to be 5.9 per cent of the total weight, while that of an adult rabbit is 2.8 per cent.

The position of the vertebrate heart is always ventral to the digestive tube, and in gill-breathing vertebrates, far anterior. When the head of a fish or a salamander is cut squarely off, the heart is usually included with it. With the development of a neck there is a backward migration of the heart in higher vertebrates, until in such long-necked forms as swans and giraffes, it comes to lie a long distance from its original location, being much more centralized with reference to the body. To have the "heart in the mouth" is, therefore, a sort of ancestral sensation that should in no way disquiet a comparative anatomist.

The adult human heart weighs not far from ten ounces, and is approximately the size of the clenched fist. It is median in position between the

lungs (Fig. 297), and not on the left side where it is popularly located by tragic actors and sentimental lovers. The reason it seems to be on the left side is because the throbbing tip of the cone-shaped ventricular part normally projects from behind the sternum towards the left side, where its kick is most readily felt.

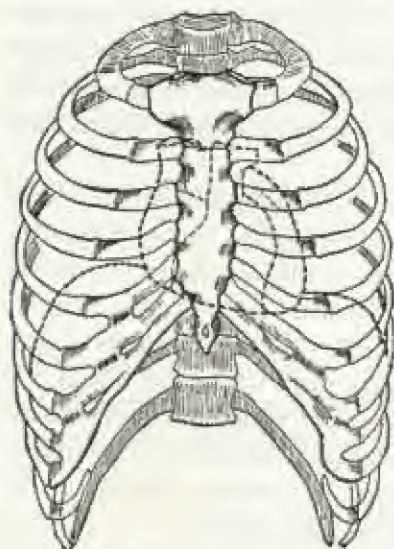


Fig. 297. Diagram showing median position of human heart, in dotted outline. (After Spalteholz.)

There are many misconceptions centering around the human heart. For instance, it is never "heart-shaped" according to the conventional Saint Valentine's outline, but instead is a flattened cone.

5. Valves

The most constant valves of the heart in the vertebrate series are the *auriculo-ventricular valves*, which separate the receiving auricle from the forwarding ventricle. They are present in all vertebrates and, in higher forms, are kept from reversing under the pressure of the contracting ventricle by tendon-like guys, *chordae tendineae*, that are anchored in the muscular walls of the ventricle (Fig. 298). There are only two such valves in the heart of fishes but in the double heart of mammals there are five present, two between the auricle and ventricle of the left side (*bicuspid valves*) and three (*tricuspid valves*) on the right side. The bicuspid valves are commonly known as *mitral valves* from a fancied resemblance to a bishop's miter. It was Huxley who once humorously said that he could always easily remember the location of the mitral valves on the *left side* of the heart because he "never knew a bishop to be on the right side."

The *semilunar valves* of the conus region are best seen in elasmobranchs and ganoids, where as many as eight rows may appear in some species (Fig. 294A and B). They are cuplike pockets, lying flat against the inner wall as the blood passes out over them, but filling immediately to block the passage-way when the blood attempts to retreat. Similar valves guard the exits from the heart to the pulmonary arteries and to the systemic aorta in the higher forms.

The primitive heart of fishes in which the sinus venosus still persists as

a distinct chamber has a pair of *sinu-auricular valves* between the sinus venosus and the atrium that, like swinging doors, allow the blood to pass to either way. This does no harm since both sinus and atrium have the common function of acting as reservoirs for returning blood.

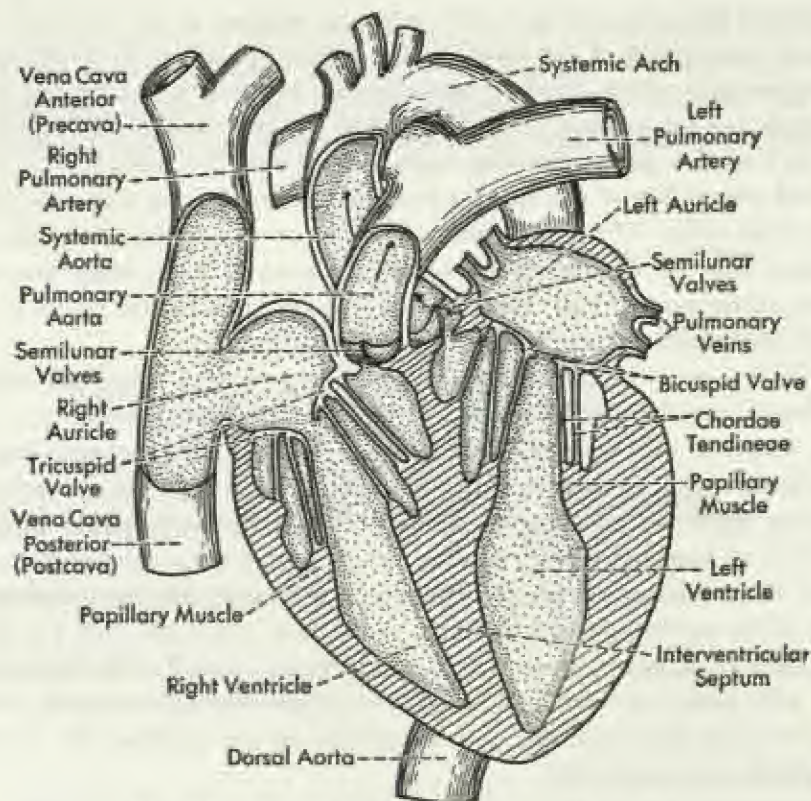


Fig. 298. Heart showing valves. (After Janmex.)

Between the atrium, or auricle, and the ventricle, on the other hand, one-way traffic must be maintained when the muscular ventricle forces out the blood, consequently mitral and tricuspid valves with their chordae tendineae, swing only so far and no farther.

6. The Work of the Heart

While compressing muscular movements of the body are largely responsible for the propulsion of lymph through the lymphatic channels, the heart is the indispensable pump by means of which the circulation of the blood is accomplished.

The blood must be kept in constant motion. That this is done is shown by the familiar fact that from any wound, however slight, which makes a break in the circulatory channels, blood immediately flows out.

In amphioxus and certain annelid worms a constant circulation is brought about simply by the contraction of arterial blood vessels, but in vertebrates generally, owing to the enormous expanse of the capillaries developed, contraction of the arterial walls is not sufficient to keep the blood in motion, and a heart becomes necessary. As has been indicated, the heart acts both as a force pump (Fig. 289), filling the arteries from the ventricles, and as a suction pump, drawing venous blood into the auricles.

The rate of flow of the blood is faster of course when an animal is active than when quiet. The contractions of the heart of a hibernating fish, for example, may fall from over 100 a minute to two or three; while that of a mouse, whose normal heart-beat is about 175 per minute, may go up to 600 per minute under the sudden stimulus of fright.

When a person is sitting quietly, about five pints of blood per minute are forced into the aorta, an amount which upon violent exercise may rise to an output of thirty-five pints per minute. Since the total amount of blood in a human adult is only ten to fourteen pints, it is evident that, while undergoing moderate exercise, all of the blood of the body passes through the heart at least twice every minute. Thus, by the most conservative estimates, the strenuous red blood corpuscles in their brief lifetime travel many miles, while accompanying leucocytes that detour constantly from the main path, like an active exploring dog on a country ramble with his master, have still more extensive locomotor adventures. Though ranging wider, they do much of it more slowly and therefore do not maintain the average rate of the red corpuscles.

Another way of reckoning the marvelous work performed normally and continuously by the human heart is to recall that with 72 beats per minute two ounces of blood are squeezed out at each beat, making the total daily output approximate 13,000 pounds. Even the heart of delicate Juliet, sighing in her balcony, did that. When a husky stevedore is forced to handle 13,000 pounds of freight in his day's work, he is honestly weary at nightfall and quite in the frame of mind to strike for shorter hours.

The constancy of the flow is aided not only by frictional resistance of the moving blood against the inside walls of blood vessels, but also by adjustable variations in pressure upon the blood stream exerted by the contractile walls of the blood vessels under the regulatory stimulus of involuntary *vasomotor nerve endings*, that act as "stopcocks" (Fig. 282). "As these terminal arteries number tens of thousands, and each of them is regulated

and controlled, one can conceive how complex the stopcock system of the human machine is" (Keith). If the varying work of the heart were not regulated by some kind of automatic device for adjusting the blood pressure and controlling the flow, disaster would inevitably follow whenever in the countless exigencies of life, a sudden extra load is thrown upon this faithful pump.

The tireless beat of the heart itself is initiated and regulated at the *sinu-auricular node* (Fig. 299). This "pace setter of the vertebrate heart" is a narrow zone of tissue that marks the transitional region between the sinus venosus and the atrium in the fish heart, and which becomes incorporated

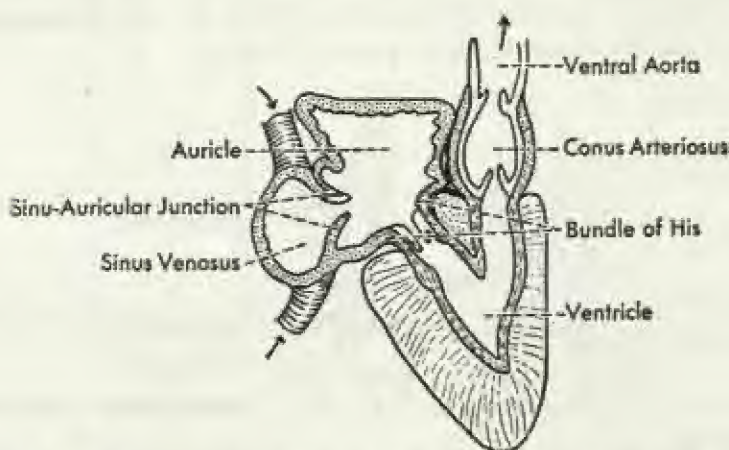


Fig. 299. Diagrammatic section of a heart to show location of timing mechanism. (After Keith.)

as a part of the auricle in higher vertebrates. Another indispensable part of the mechanism of the throbbing heart is the *auriculo-ventricular node*, a dense network of cardiac muscle fibers connecting the auricular and ventricular walls, and acting somewhat like the "timer" in an automobile. Across this bridge the initiatory stimulus, originating in the sinu-auricular node, is transmitted to the ventricle completing the heart-beat. The auriculo-ventricular node was discovered in the human heart by His in 1893, and is consequently known as the *bundle of His*.

Although the heart beats in successive throbs, a constant flow of blood is maintained because the elastic arteries, stretched by the pressure generated by the ventricular contraction, gradually contract until they are suddenly distended again by the next "beat" of the ventricle. There is thus a constant flow of blood from arteries into capillaries.

VI. ARTERIES AND THEIR TRANSFORMATIONS

In arteries, as already indicated, the blood flow is away from the heart, making the outward delivery trip of the things needful from the source of supplies to the capillaries. This object is attained in all vertebrates by means of one fundamental scheme of pathways, although the general plan is modified to meet the demands of different types of vertebrates. Once the main trunk line of the dorsal aorta emerges from the complexities of the arterial arrangement in the head and gill region, further distribution to the various organs of the body of arteries branching off from the aorta is fairly uncomplicated and uniform throughout the vertebrate series. The anterior arteries of the gill region that bear the brunt of the transformation from water to land life, however, show greater diversity.

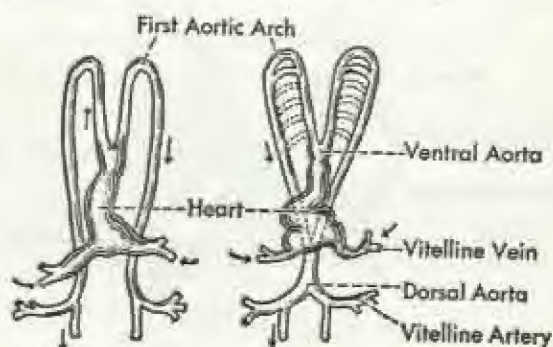


Fig. 300. Diagrams illustrating the arrangement of the primitive heart and aortic arches. *a*, early stage; *b*, later stage. (After Heisler.)

In amphioxus the *ventral aorta*, or the main blood vessel anterior to the liver diverticulum (Fig. 277), is connected with the dorsal aorta by a number of pairs of lateral loops that encircle the anterior part of the digestive tube. There may be as many as sixty pairs of these loops in the adult animal, occupying a large portion of the anterior part of the body. Each pair is interrupted by the insertion of gill capillaries in which the blood takes on oxygen from the surrounding water.

In true vertebrates the number of pairs of branchial loops, although less in the adult, is typically six during embryonic development, with the exception of certain primitive sharks, for example *Hexanchus* which has seven, and some cyclostomes which exceed the typical number. The first pair is laid down as part of the original vitelline circulation (Fig. 287). Subsequently five additional pairs are laid down one after the other, beginning with the most anterior one (Fig. 300).

The usual embryonic arrangement of these branchial arterial vessels, as indicated in Figure 301, may be taken as a point of departure for the adaptations to follow in the different vertebrate classes.

It will be seen that the branchial loops do not connect directly with the main dorsal aorta but first join with two smaller blood vessels, the *radices aortae*, which secondarily join, like the converging arms of the letter *X*, to make the single dorsal aorta.

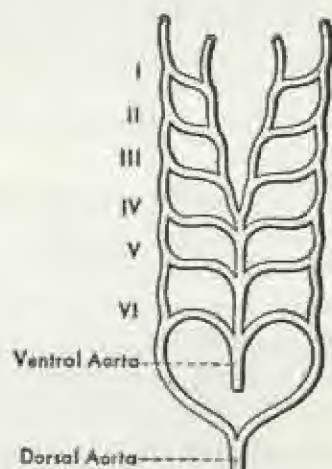


Fig. 301. Theoretical plan of embryonic arterial loops. (After Boas.)

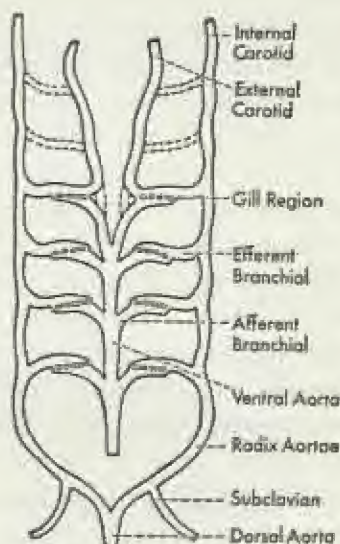


Fig. 302. Plan of arterial loops in fishes.

In *fishes* (Fig. 302), the two most anterior pairs of loops, that are supported by the mandibular and hyoid arches of the splanchnocranium, are reduced to branches of the third in adult life, leaving the remaining four to become the branchial arches, interrupted by the capillaries of the *internal gills* as they pass from the ventral side to the *radices aortae*.

In *urodele amphibians* (Fig. 303) *external gills* are introduced which, unlike the internal gills of fishes, do not directly interrupt the branchial loops but are established on a detour from the loops (Fig. 328), so that it is possible for the blood to pass from the ventral to the dorsal aorta by either of two routes, one through the uninterrupted branchial loop in which no capillaries are present, and the other by way of a side line through the capillaries of the external gills.

Three pairs of such external gills, situated on loops IV, V, and VI, may be present in urodeles. Thus in those salamanders that discard their

gills during metamorphosis, it is possible for the blood to progress without interruption by way of the branchial loop direct, avoiding the disastrous consequences which would inevitably result if a single unavoidable route through the internal gills, as in fishes, were put out of commission.

In urodeles, it should be noticed that the last and most posterior loop (VI) has its ventral portion pressed into the service of the *pulmonary artery* which goes to the newly-established lungs, for the oxygen-supply, instead of directly to the dorsal aorta. The dorsal part of this loop is reduced to a *ductus arteriosus*, or *duct of Botallus*. In all amniotes this duct functions until hatching or birth and its ghostly remains still haunt the arterial complexes of higher vertebrates, even of man, serving as a reminder of emergence from water to land life. Furthermore, in urodeles loop V and that part of each radix aortae between loops III and IV, in anticipation of their later obliteration in anurans, become much attenuated.

The *anurans*, represented by the frog (Fig. 295), pass through a youthful tadpole stage in which their branchial arteries resemble those of urodeles, but they go a step further in burning their ancestral arterial bridges behind them, since only three pairs (III, IV, and VI) of the six original embryonic loops survive in the adult. Loop IV becomes the large graceful paired systemic arch, while loop III is entirely devoted to supplying the head region. Since the connectives of the radices aortae that run between loops III and IV are suppressed, the blood in the third loop can no longer pass backward directly into the dorsal aorta. Loop V, already showing signs of degeneration in the perennibranchiate urodeles, disappears entirely in adult frogs, as does the dorsal part of loop VI, the ventral part of which persists as the *pulmocutaneous artery*.

In *reptiles* three pairs of loops, namely, III, IV, and VI, survive (Fig. 304). With the beginning of a separation of the ventricle into two parts, the ventral aorta near the heart splits, not into two but into three parts, two of which go with the right ventricle and the third with the left one. Of the portions draining the right ventricle, one connects with only loops VI to become the *pulmonary aorta* while the other leads into the left aortic arch IV as the *left systemic aorta*. The division of the ventral aorta draining the left ventricle sends blood forward into the carotids and also through the right fourth loop, *right systemic aorta*.

In amphibians the mixture of aerated and non-aerated blood occurs in the single ventricle of the heart before it is sent out over the IVth arterial loop, but in reptiles, which have at least a partial partition established between the ventricular chambers of the heart, the mixing of "pure" and "impure" blood may be postponed until the right and left branches of

loop IV pour their diverse contributions into the common dorsal aorta. Reptiles as well as amphibians are "cold-blooded," one contributing reason being that in both cases some of the blood that has not been oxygenated is poured back into the dorsal aorta and sent again "unpurified" over the body. The result, like mixing clinkers with coal, is that the fires do not burn any too brightly and cold-bloodedness follows.

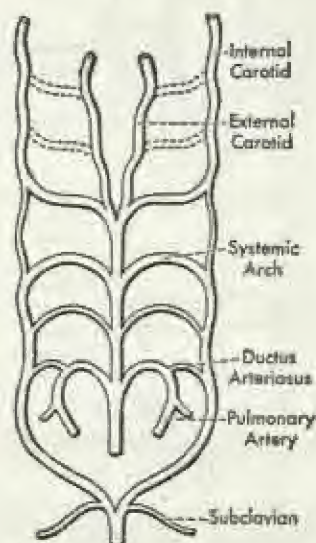


Fig. 303. Plan of arterial loops in urodeles. (After Boas.)

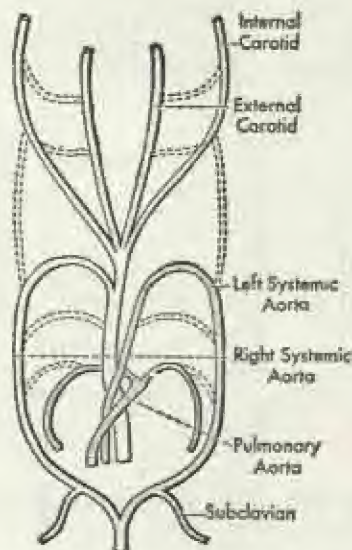


Fig. 304. Plan of arterial loops in reptiles. (After Boas.)

Birds, which arose from an advanced reptilian stock, follow the general reptilian pattern but they discard the left systemic aorta (Fig. 305). Thus the right fourth loop and accompanying radix aortae form the single systemic arch. This important change results in all of the blood pumped by the right ventricle going to the lungs, none of it becoming mixed with the blood which is sent out from the left ventricle to all of the other organs of the body.

Mammals, derived from a primitive reptilian stock before major modifications in the direction of the modern reptilian plan, have both right and left fourth loops connected with the portion of the ventral aorta leading from the left ventricle (Fig. 306). In mammals it is the left fourth loop and accompanying radix aortae which persist as the systemic arch while the right fourth loop becomes the beginning of the right subclavian artery.

Thus in man a single large aortic loop, like a shepherd's crook, arises

from the heart, arches over to the left, and passes backward to supply the body and its various organs. This loop is the combined product of (1) the embryonic ventral aorta; (2) the left side of the IVth branchial loop; and (3) the left arm of the radices aortae.

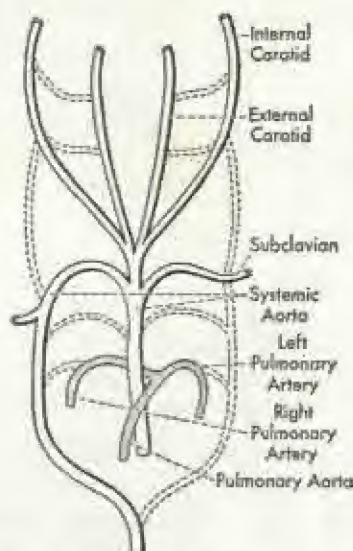


Fig. 305. Plan of arterial loops in birds. (After Boas.)

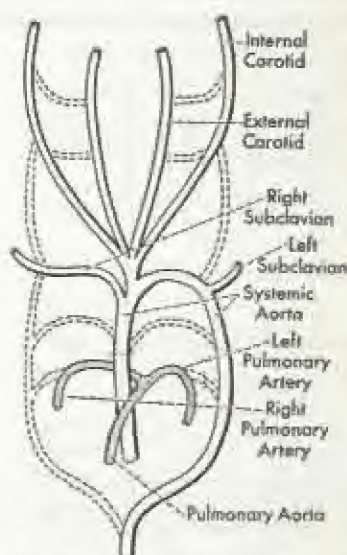


Fig. 306. Plan of arterial loops in mammals. (After Boas.)

Occasional rare cases, reported in medical literature, of double aortic arches in man, or of the aortic arch on the right side as in birds, find a ready interpretation in the light of comparative anatomy.

VII. VENOUS ROUTES

I. In General

The channels by means of which the blood is collected and returned to the heart have undergone a greater degree of evolutionary adaptation in the vertebrate series than the corresponding arteries that distribute the blood over the body from the heart. This is due in part to the elaborate complexes of capillaries inserted in the course of the veins which form the "portal systems," and in part to the accessory services of the lymphatic system of channels.

As would be expected the least complicated arrangement of veins is found in *amphioxus* (Fig. 307). Blood from the body wall is picked up by

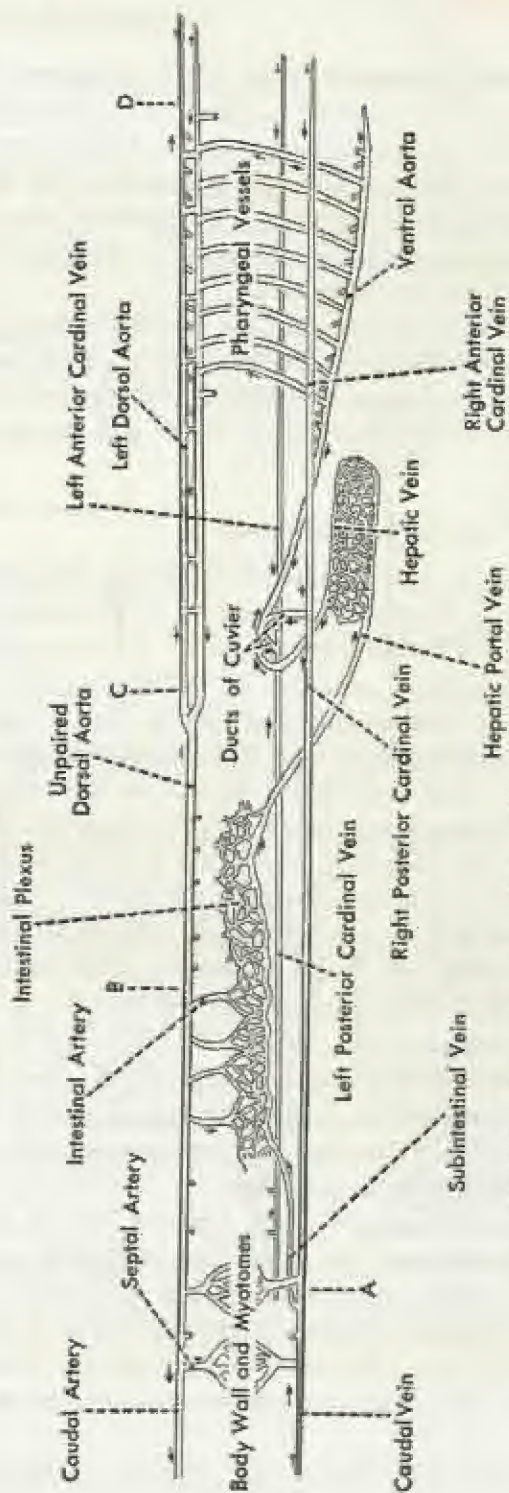


Fig. 307. Circulation of amphioxus, diagrammatic. Arrows indicate direction of flow of the blood. a, level of anus; n, level of notochord; p, level of pharynx; v, level of velum; c, level of atriopore; d, level of posterior end of pharynx. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

paired *anterior* and *posterior cardinal veins* which communicate with the ventral aorta by means of the *common cardinal veins*, or *ducts of Cuvier*. An unpaired *caudal vein* picks up blood from the postanal region of the body and, near the anus, joins both the right postcardinal and the *subintestinal vein*, which continues forward beneath the intestine, not only receiving contributions from the capillaries that encircle the alimentary canal, but also deriving food from the canal itself.

Upon reaching the liver diverticulum the subintestinal vein breaks up into capillaries, thus establishing a primitive hepatic portal system. The *hepatic vein*, from the liver, is soon joined by the common cardinals to form the *ventral aorta*, which carries blood to the gills and is destined to evolve into the heart.

2. Development of Veins in Elasmobranchs

A brief survey of the main steps in the development of the veins in elasmobranchs will aid us in a better understanding of the adult plans of not only the lower fishes but vertebrates in general. At least seven of these major steps may be recognized, namely, (1) vitelline stage, (2) subintestinal stage, (3) common cardinal stage, (4) hepatic portal stage, (5) subclavian stage, (6) subcardinal stage, and (7) renal portal stage (Fig. 308).

A pair of *vitelline veins* entering the body from the yolk sac, as described in section IV, is the first evidence of the venous system. They run forward ventral to the digestive tract, passing first along the duodenal region where the liver is soon to grow out ventrally (Fig. 265).

Soon a *subintestinal vein*, usually connecting with the left vitelline vein, develops along the ventral side of the posterior part of the intestine and into the tail, after looping around the cloacal region.

Paired *common cardinal veins*, or *ducts of Cuvier*, each formed by the union of an *anterior cardinal* from the head region and a *posterior cardinal* from the body wall posterior to the heart, next appear. At this time anastomoses between the vitelline veins form two venous rings, the anterior one looping around the small liver diverticulum.

As the liver outgrowth increases in size it pushes into the anterior vitelline loop, gradually breaking up the vessels here until they are reduced to capillary size. In this manner there is established an *hepatic portal system* which in this stage begins in capillaries in the tail region as well as in the wall of the digestive system. The anterior parts of the vitellines, which carry blood from the liver to the sinus venosus, now become known as the *hepatics*.

The next new vessels to develop are the *subclavian veins*, leading from

the anterior fin buds to the common cardinals, and the *ventral abdominal veins* running along the ventral abdominal wall to empty into the subclavians. Meanwhile the posterior cardinals have grown back until they have joined with the cloacal loop and the subintestinal vein has subsequently broken away from this loop. The hepatic portal system is now limited to the draining of the digestive system, as in adult animals.

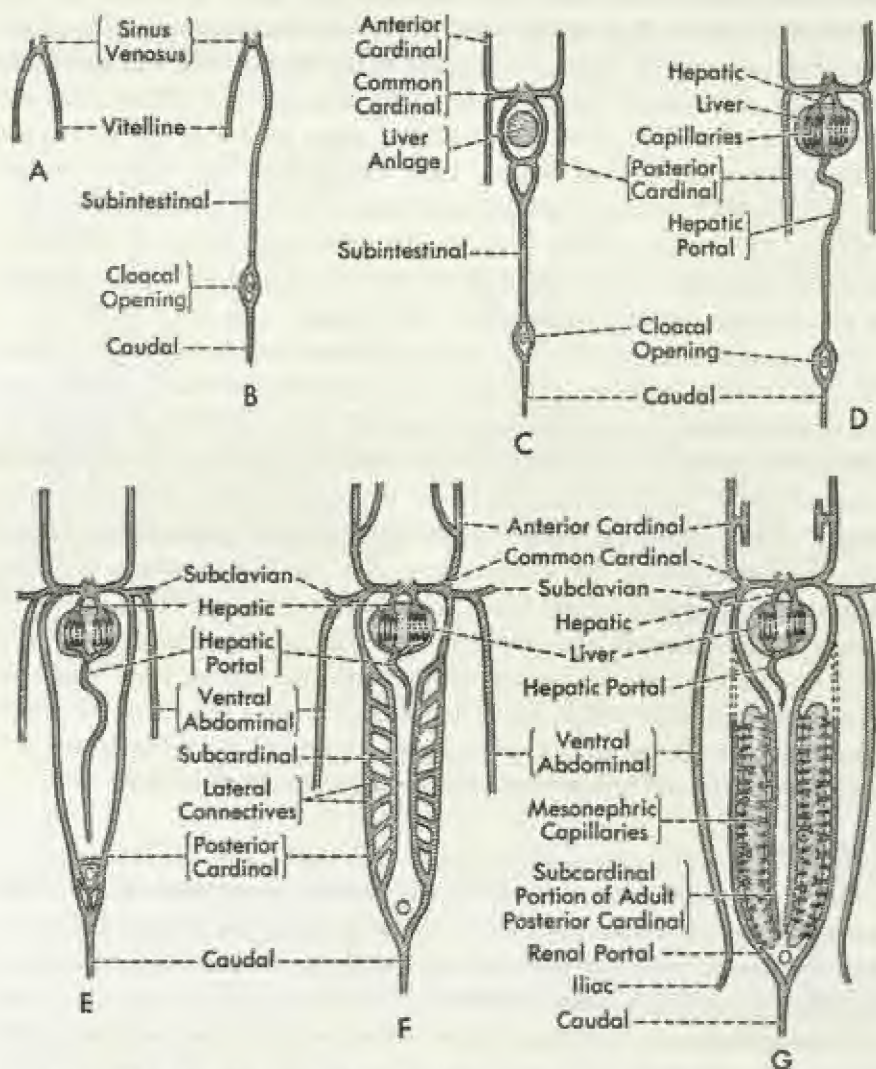


Fig. 308. Development of veins in elasmobranchs, diagrammatic. A, vitelline stage; B, subintestinal stage; C, common cardinal stage; D, hepatic portal stage; E, subclavian stage; F, subcardinal stage; G, renal portal stage. (After Hochstetter and Hyman.)

Between the developing mesonephroi there next appears a pair of *subcardinal veins*, each with numerous lateral connections between it and the corresponding posterior cardinal. Gradually portions of all except the most anterior pair of these connections are broken up into capillaries in the mesonephroi.

Finally, the posterior parts of the posterior cardinals become the *renal portal veins* as they break away from their anterior parts. As a result of this separation the adult plan of veins associated with the mesonephroi is established. The renal portal system, composed of the caudal vein and two renal portal veins, takes blood from the tail to the mesonephroi. Blood from the mesonephroi is carried to the heart by the veins known in adult animals as the posterior cardinals, despite their embryonic origin from several sources, including a pair of subcardinals and a pair of lateral connections as well as the anterior parts only of the embryonic posterior cardinals. Meanwhile the ventral abdominal veins, growing posteriorly, have extended into the posterior fin buds as the *iliac veins*.

By these various steps the *adult plan of elasmobranchs* has been reached (Fig. 308c). Two pairs of large veins enter the heart, namely the *hepatic veins* from the liver and the *common cardinal veins*, into which empty the posterior cardinals, anterior cardinals and subclavians. From the tail region the *renal portal system* carries blood to the mesonephroi where it passes through capillaries and is picked up by the *posterior cardinals* which also drain the dorsal part of the trunk region. The *anterior cardinals*, aided by much smaller *jugulars*, return blood to the heart from the head. The *subclavians* drain not only the pectoral appendages and neighboring body wall, but also, through the *ventral abdominals*, the ventral body wall and, through the *iliacs*, the pelvic appendages. Blood from the digestive system is picked up by the *hepatic portal system*, carried to the liver where it is strained through capillaries, and picked up by the hepatic veins.

3. Evolution

In the larger group of bony fishes the venous arrangement is much like that of the cartilaginous elasmobranchs, except that the ventral abdominal veins disappear, and the traffic from the body wall and pelvic fins is shunted over to the posterior cardinals.

Salamanders and frogs, as representative amphibians, present further stages in the evolution of vertebrate veins, which can be interpreted by comparison with the more generalized arrangement already described for elasmobranch fishes.

The plan of the principal veins in salamanders, as shown diagrammat-

ically in Figure 309A, presents three striking innovations. First, there appears a new vein, the *postcava* or *vena cava posterior*, that rivals the anterior portions of the posterior cardinals, collecting their blood from the mesonephroi. Arising embryonically from the hepatic veins, this important blood channel grows back through the liver and then along the dorsal body wall near the dorsal aorta to join the postcardinals where they fuse near their junction with the subcardinals, at the anterior ends of the mesonephroi. It increases in size until it takes over most of the transportation from the abdominal cavity to the heart.

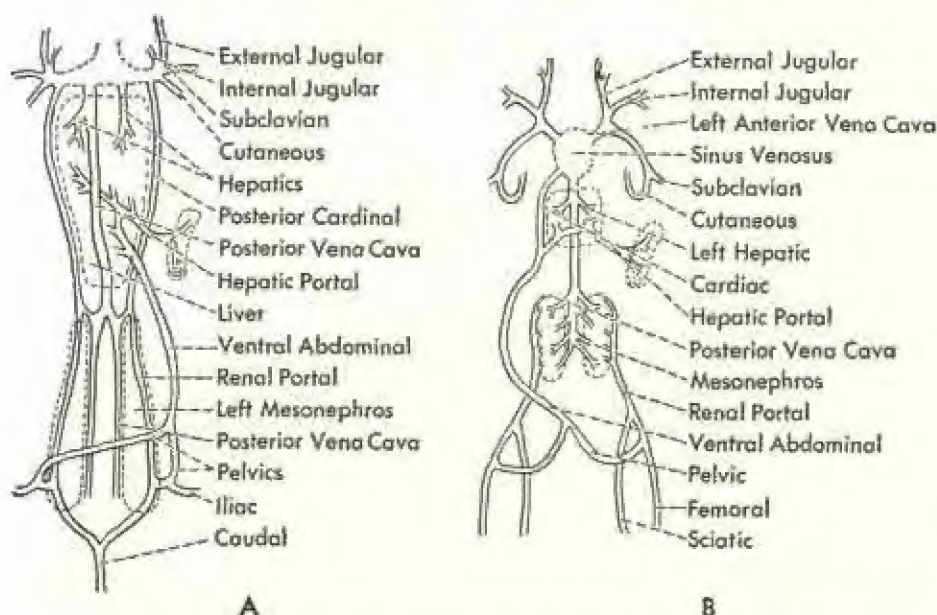


Fig. 309. Diagrams of the venous systems of (A) a urodele and (B) a frog. Left auricle and pulmonary veins not shown.

Secondly, the iliac veins fork, each sending one branch to its renal portal, while the other branch, representing the ventral abdominal vein of the elasmobranch, fuses with its fellow to form a median *ventral abdominal vein* that empties anteriorly into the hepatic portal vein. Blood returning from the hind legs of an amphibian, therefore, may pass through either the renal portal or the hepatic portal capillary strainer before reaching the heart, whereas in fishes the iliac blood goes directly to the heart by way of the ventral abdominal veins without portal interference of any kind.

Thirdly, amphibians, as lung breathers, develop a pair of *pulmonary veins*. The pulmonary veins are not represented in these figures which show

only the veins emptying into the sinus venosus or right auricle. Because amphibians use the skin to a considerable extent as a supplementary breathing organ, they have in addition a pair of well-developed *cutaneous veins*, from the skin, which join the subclavians. Diagrammatically these bear a superficial resemblance to the lateral veins of elasmobranchs but should not be confused with them.

The arrangement of the veins in a frog embryo, or tadpole, is like that of a salamander, except that the rivalry between the newly established postcava and the diminishing posterior cardinals culminates in the case of the frog tadpole in the successful monopoly of the circulatory blood traffic by the former and the disappearance of the latter (Fig. 309B). With the elimination of the posterior cardinals, the anterior cardinals become single, continuous channels with the ducts of Cuvier, forming veins now called *precavae* (*venae cavae anteriores*) into which the *jugular veins* empty to return blood from the head directly into the right auricle of the heart. In the frog the iliacs are represented by *femoral* and *sciatic* veins, the femoral splitting to enter the renal portal (postcardinal) and abdominal, and the sciatic entering the renal portal. Though the tail is lost, there is no consequent loss of the renal portal. Such drastic changes as these, designed to meet the difficult conditions accompanying the precarious transitional method of their life, are typical of the many bodily makeshifts which this small struggling group of vertebrates has had to resort to in order to accomplish the great evolutionary feat of emerging from water to land.

The degenerating posterior cardinals become replaced in reptiles by a pair of longitudinal *vertebral veins* (Fig. 310A), that involve anastomoses of *intersegmental* and *intercostal veins*.

In the head region of lizards, snakes, and turtles, as pointed out by Bruner,* the venous system is characterized by an abundance of *sinuses* or blood-filled enlargements of the veins, both inside and outside of the cranium. Through a modification of the blood pressure in the superficial sinuses that extend over the skull beneath the skin, the molting (ecdysis) of the corneal layer over the head is facilitated. Recourse to such a loosening device as these sinuses is advantageous in the case of these reptiles because their thick dry integument, which is particularly tight over the head, does not easily allow for ecdysis. In *Phrynosoma*, the "horned toad" of the cactus regions of southwestern United States, the venous sinuses, together with associated muscles, form a curious protective mechanism whereby these grotesque animals under excitement are able to squirt blood from their eyes by way of ruptured sinuses of the *orbital veins*. Modifications of

* *Amer. Jour. Anat.*, v, VII, 1907.

the head veins are much less in evidence in the Crocodilia than in the three lower groups of reptiles just mentioned. In fact the Crocodilia deviate markedly in many particulars from all other living reptiles and may possibly be regarded as anatomically the evolutionary advance-guard of the reptilian army.

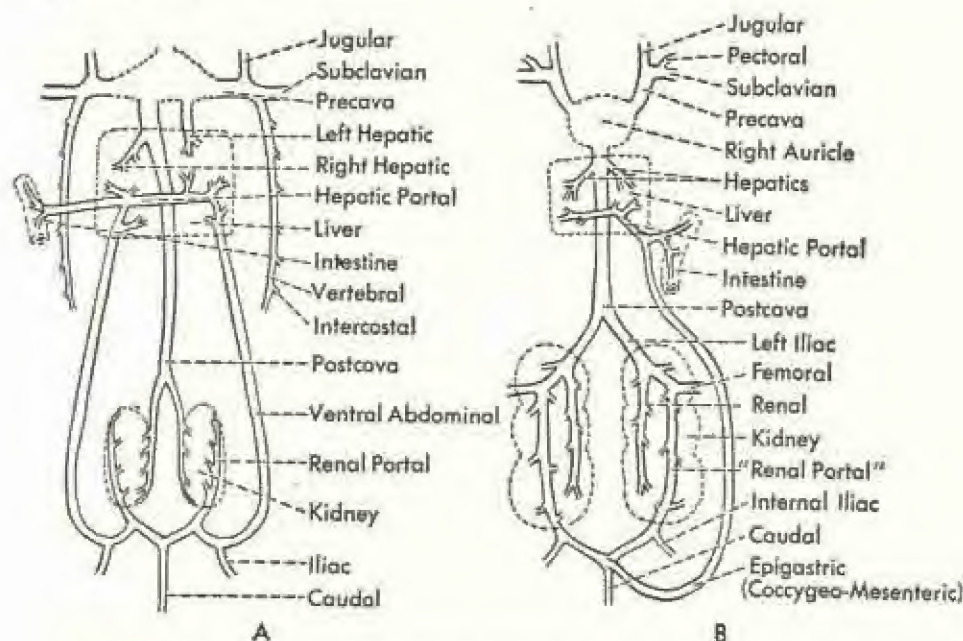


Fig. 310. Diagrams of the venous systems of (A) a reptile and (B) a bird. Left auricle and pulmonary veins not shown.

The renal portal system, although possibly persisting in modified form in reptiles, disappears in birds, with the loss of a muscular tail, while the abdominal vein of amphibians and reptiles merges in birds into an *epigastric vein* (Fig. 310B), which is possibly homologous with the embryonic *umbilical vein* of mammals.

The lost renal portal system is not recovered in the higher vertebrates, even in those species that possess well-developed tails (Fig. 311).

The venous system of mammals is further characterized by the introduction of certain novelties. The persisting anterior end of the right posterior cardinal vein, together with remnants of the transient *supracardinal* and *subcardinal* parallel to it, becomes the *azygos vein*, while a fragment of this complex on the left may join forces as the *hemiazygos vein* in the more posterior part of the body. The azygos and the hemiazygos veins are connected by transverse anastomosing bridges into the *azygos system*.

In marsupials, rodents, insectivores, and many artiodactyls, the azygos system is about equally developed on the two sides, while in the head region two precavas still persist to return blood to the heart in balanced fashion (Fig. 311A). In edentates, carnivores, and primates, on the other hand,

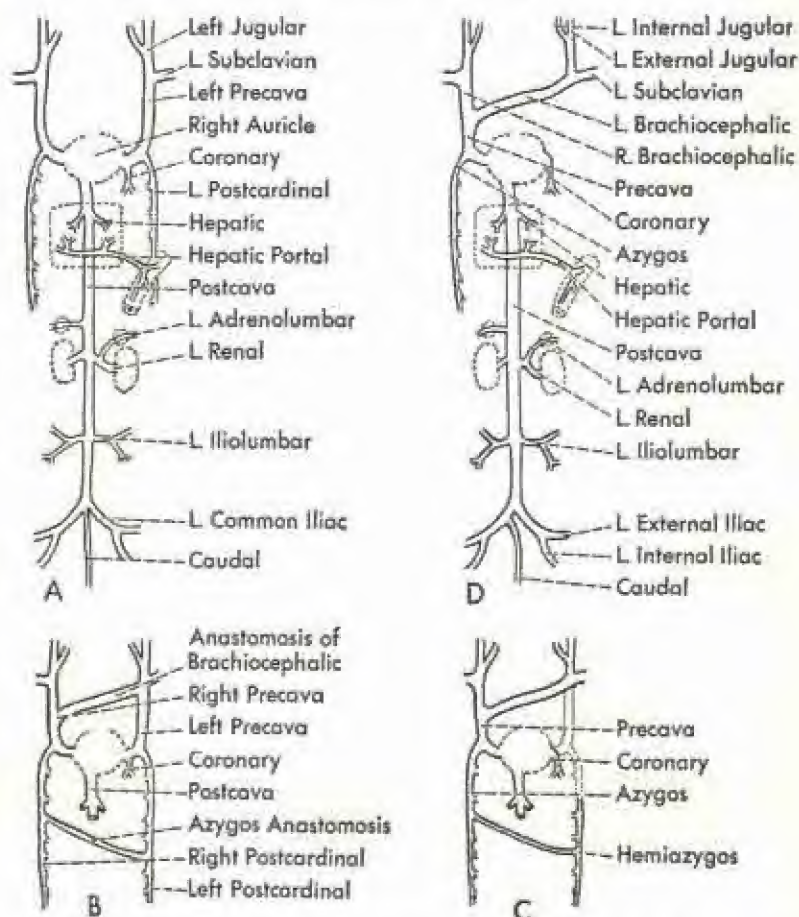


Fig. 311. Diagrams of the venous systems in mammals. A, lower mammalian plan; B, embryonic stage of anterior vessels in higher mammals; C, anterior vessels of those higher mammals which retain part of left postcardinal, showing in dotted lines the parts which disappear; D, venous plan of those higher mammals which lose the hemiazygos.

a reduction of the azygos system on the left side results in an asymmetrical shifting of most of the blood from this area to the right side for delivery to the heart, while in the head region the right precava becomes dominant in the following manner. A cross-vein, the *left brachiocephalic*, is laid down from the right precava diagonally across and forward to the left precava

at the point where the latter is formed by the union of jugular and subclavian (Fig. 311b). The left precava between this cross-vein and the heart then degenerates except for a small part, the region of the original duct of Cuvier, which persists as the *coronary sinus* through which blood from the wall of the heart is emptied into the right auricle. The part of the right precava in front of the cross-vein is now known as the *right brachiocephalic* while the posterior part remains as the single precava which empties into the right auricle after receiving the *azygos vein*, the original right postcardinal (Fig. 311c).

Not only the heart but all of the larger blood vessels, arteries, veins, and lymphatics, are supplied in their outer walls (tunica adventitia) with a ramifying system of nutrient blood vessels, called *vasa vasorum*, or "vessels of the vessels," for just as "shoemaker's children must also have shoes," so blood vessels need to be provided with a supply mechanism of their own.

VIII. LYMPHATICS

The essential points to find out about the elusive ghostly lymphatics are their extent and relation to the tissue spaces of the body, which are not empty at all but instead are filled with various fluids, the more important of which are (1) *plasma*, confined within the closed haemal system of arteries, veins, and capillaries; (2) *lymph*, carried within the lymphatic vessels, which is much like plasma but is without red corpuscles; (3) *tissue fluid*, which is plasma that has seeped out of the main blood stream and bathes the cells of most of the tissues much as the waters of a swamp surround soil particles and keep them moist; (4) *cerebro-spinal fluid* in the subarachnoid spaces around the central nervous system which contains certain products of internal secretion and is different from the lymph in the lymphatic channels; and finally (5) the fluid in the aqueous chambers of the eye, and that in the inner ear which, although described by the terms *endolymph* and *perilymph*, has no direct connection with the lymphatic system.

The anastomosing network of the *lymph channels*, which are crocheted all around the other blood vessels (Fig. 312), is anatomically and physiologically distinct from the much more easily seen arteries, veins, and capillaries of the haemal system through which the red blood flows. They probably equal if they do not exceed the haemal system in total carrying capacity although they do not extend everywhere throughout the body.

To quote Dr. Sabin who is an outstanding authority in this phase of anatomy: "Lymphatics have not been demonstrated in the adult liver

beyond the capsule and the connective tissue septa, nor in the spleen beyond the capsule. It is well known that lymphatics are abundant in tendons; but that they have not been demonstrated in striated muscle. On the other

hand, it has been definitely shown, both in the embryo and in the adult, that there are no lymphatics in the central nervous system."

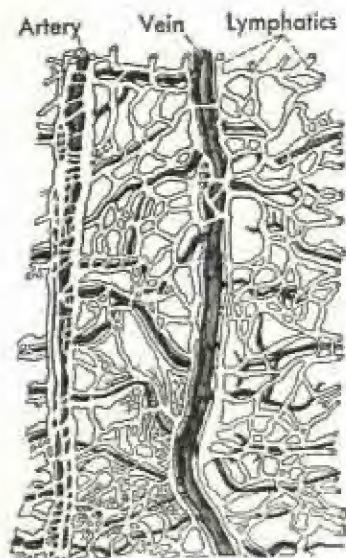


Fig. 312. Lung of *Necturus* with the blood and lymph vessels injected. The lung was cut open, spread out flat, and mounted in balsam. Only the main branches of the artery and vein are shown. The blood and lymph vessels were drawn by means of the camera lucida and show the exact relations of both sets of vessels. (After Miller.)

The lymphatic vessels of the digestive tract, which project into the innumerable villi of the small intestine, are known as *lacteals* because the absorption by them of the fatty products of digestion results in an emulsion that gives to them a white milk-like appearance.

Lymphatic channels vary in size from minute varicose capillaries where transfer of materials takes place, to large *ducts* and *sinuses*. Under the loose skin of a frog there are extensive lymph reservoirs in the form of subcutaneous sacs (Fig. 313) which, like a wet blanket, protect the underlying tissues from excessive loss of water during the temporary excursions of this amphibian from water to land.

Unlike red blood, lymph always travels toward the heart, backsliding being prevented by numerous pocket-like valves like those in certain veins, which allow forward movement but prevent retreat. While the

flow of lymph is accomplished in some degree by gravity, its advance is principally brought about by the muscular movements of the exercising body, by means of which it is squeezed along its one-way course toward the heart.

Since the lymphatic channels in the adult are not incorporated in the closed circuit of the haemal system, the pumping power of the heart, being an integral part of the haemal system, can have no effect upon lymph movement.

In the lower vertebrates the larger lymph channels may acquire muscular walls and become pulsating *lymph hearts*, thus supplementing by their contraction the body muscles in the forward movement of the lymph. Among amphibians the caecilians (Apoda) have a pair of lymph hearts

for each of the numerous segments of their elongated wormlike bodies, while urodeles likewise possess a double row of several lymph hearts, situated along the posterior part of the lateral line on either side. Frogs, and their relatives, typically have four lymph hearts in adult life, situated at



Fig. 313. Subcutaneous lymph sacs of a frog. The skin is represented as removed and the sacs are outlined by lines of connective tissue that join the skin to the underlying muscles. (After Gaupp.)

four busy centers with reference to the legs and arms (Fig. 314). The anterior pair are at the level of the third vertebra near the junction of the subclavian and jugular veins at the base of the arms. The posterior pair are at the base of the iliac veins in association with the blood supply of the legs on the dorsal side to the right and the left of the *urostyle* and can easily be seen throbbing under the skin of a live frog.

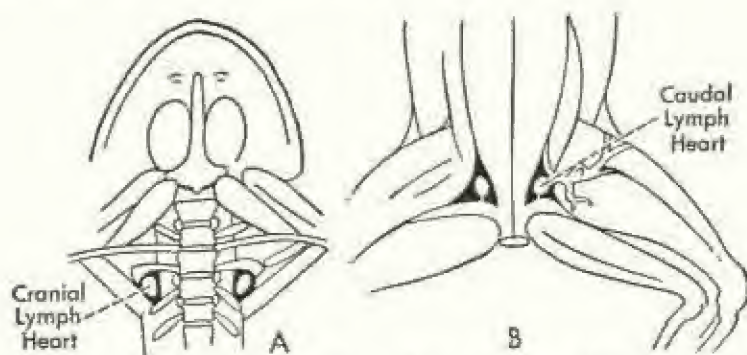


Fig. 314. Lymph hearts in a frog, *Rana*. A, antero-dorsal region; B, postero-ventral region. (After Schimkewitsch.)

In reptiles only the posterior pair of lymph hearts typically persist, while in birds and mammals even these vanish after a reminiscent embryonic appearance.

Added to the regular lymphatic channels and their modifications in the form of enlarged sinuses and pulsating hearts, there are present through-

out the lymphatic system, particularly in mammals, numerous *lymph nodes*, as well as certain localized tissues and organs of a predominantly lymphoid character, such as the bone marrow, the "fat bodies" of hibernating animals, tonsils, Peyer's patches in the small intestine, and the spleen.

Lymph nodes are usually encapsuled, with an internal mesh of connective tissue in which leucocytes are lodged. They are supplied with in-current and ex-current lymph vessels, the former being more numerous than the latter. In these nodular substations not only is the filtering of solid materials in the lymph accomplished, but also tarrying leucocytes may there undergo dissolution and removal, as well as renewal by mitosis.

The largest and most constant of the lymphatic organs is the *spleen*, which lies encapsuled in the body cavity of vertebrates. It attains an average weight of seven ounces in man and upon occasion may be extirpated without fatal results. The exact function of the spleen is so problematical that no statement with reference to it has ever gone uncontradicted. The ancients were quite at sea regarding it. Hippocrates, the Father of Medicine, says that "it draws the watery part of the food from the stomach." The great Aristotle could only guess that it is a "prop for the stomach," while Galen, who was the prime authority in anatomy for centuries, oracularly declared that its function is "to keep the body warm." In more recent times, with almost equal vagueness, word goes forth that "it is generally believed that this organ shares with the lymph tissues in the formation of lymphocytes, and is also concerned in the destruction of waste red blood corpuscles." The ambitious student with an itch for discovery may be gratified to know that there are still left many little known regions awaiting exploration beyond the horizon.

The largest of the lymphatic vessels is the *thoracic duct*, into which the others posterior to the diaphragm and on the left side of the anterior part of the body empty. It opens into the venous system at the junction of the left jugular and left subclavian veins. The *right lymphatic duct*, which receives all lymphatics from the right anterior part of the body, empties into the right subclavian vein. In mammals, although embryonically paired, only the left thoracic duct persists.

The lymphatic channels arise from the haemal blood vessels, as has been demonstrated by Dr. Sabin, and not independently in the interstices of the tissues as formerly thought. Endothelial buds from the walls of the capillaries grow out and make a centrifugal invasion of the entire body, eventually becoming disconnected from the closed haemal system except at the points where the thoracic duct and the right lymphatic duct connect with the veins in the neighborhood of the heart.

The lymphatic capillaries forming as outgrowths of the endothelial buds are thus *closed at their distal ends* and do not open freely into tissue spaces. The return of the lymph from these spaces to the thin-walled lymphatic capillaries, therefore, like its escape from the haemal capillaries, is by the process of seepage and diapedesis and not by direct entry into open ends of lymphatic vessels.

The Release of Energy—Respiratory System

I. IN GENERAL

1. The Respiratory Environment

Every living thing of which we have any knowledge exists on the planet earth at the bottom of a vast atmospheric ocean. Air envelops not only all land surfaces but extends also to the uttermost depths of every body of water, large or small, so that aquatic as well as terrestrial animals and plants find themselves bottom-dwellers with respect to the all-inclusive atmosphere.

Air not only presses on all the external surfaces of the body at approximately fourteen pounds to the square inch, but also envelops the internal surfaces of the lungs. The oxygen contained in the air forms the indispensable setting for the drama of life. Ordinarily the amount present is about 21 per cent by volume, while approximately 78 per cent is free nitrogen, an inert gas which dilutes oxygen to livable proportions.

Although the large amount of free nitrogen in the air plays no direct part in respiration, it is a most important chemical component of the protein compounds that make up living matter. It is not, however, available for use as protoplasm-building material in its abundant free form, but must undergo a sequence of chemical combinations through the agency of plant life before it can finally be incorporated in the animal body.

The mixture of oxygen and nitrogen which we call air is essential to life. It is said that a dog can live three months without food, three days without water, but only three minutes without air. Of all known organisms only the extremely specialized group of anaerobic bacteria seem to be able to live without the oxygen of the air, and even they obtain it by the chemical break-up of their own bodily structure.

Although the atmospheric envelope is enormously extensive in every

outward direction, the only part of it occupied by living things is comparatively the merest film in thickness, where the atmosphere comes in contact with the solid earth. The greatest vertical distance from the atmospheric floor reached by any organism has been attained by modern human aviators, who in order to outstrip soaring birds have had to include in their equipment a supplementary supply of stored oxygen. The exceptional altitudes gained by human pioneers of the air must be regarded as insignificant in extent when compared with the distances involved in the horizontal exploration of the earth's surface.

Probably eighty per cent of all known animals breathe *free air*. This category includes mammals, birds, reptiles, many amphibians, some fishes; the great fraternity of tracheate arthropods, besides certain gastropods among the mollusks, and some annelids. Strictly, however, no animal breathes "free air," since a water film is necessary for every respiratory surface. In the minority innumerable aquatic invertebrates, fishes, and perennibranchiate amphibians habitually breathe air that has been *dissolved in water*, that is, air which occupies the invisible interstices between molecules of water. Some animals, for example whales and pulmonate snails, live habitually in water but come periodically to the surface for free air, while a few exceptional land animals, such as the terrestrial isopods and land crabs, still retain at an obvious disadvantage the primitive aquatic method of taking air in water by keeping their gills moist, although they have deserted water as a medium in which to live.

Since there is considerably more oxygen in free air than is dissolved in water, free-air breathers in general exhibit more energy than aquatic forms, living as they do in a more favorable respiratory environment. As a matter of comparison sea water contains five to seven cubic centimeters of oxygen per liter; flowing fresh water, six to eight cubic centimeters; and free air over 200 cubic centimeters per liter.

2. The Exchange of Gases

When the Declaration of Independence was signed no one knew that life processes are due to a form of slow combustion, dependent upon a component in air called *oxygen*. Lavoisier made this clear for the first time in 1777. In 1794 he was guillotined by his unappreciative fellow countrymen as "one of the enemies of the country." Thus politics dominates science.

The exchange of gases which we term "breathing" is primarily a physical rather than a biological phenomenon. The taking in of oxygen is a process of passive diffusion that ceases as soon as the oxygen within the

cells concerned balances with that outside. As a result of taking in oxygen, tissues are slowly broken down, while the energy used to build them up is released, much as "stored sunshine" from plants of the Carboniferous Period is recovered in the form of heat energy whenever these fossils which we call "coal" are burned under a draft of air. In both burning coal and living body the most conspicuous product of combustion is *carbon dioxide*. This is given off directly, since it acts as a poison when retained. In fact the removal of carbon dioxide is so urgent a matter that no animal can "hold its breath" very long without being compelled by an imperative stimulus quite beyond its control, to resume breathing movements. This powerful stimulus, which insures the continuous working of the mechanism of respiration, is due to an excess of carbon dioxide in the blood acting upon a reflex center in the medulla of the brain.

Unlike food, neither the carbon dioxide of metabolism nor the oxygen of the air can be stored within the body. Consequently, although respiration can be reduced to a minimum during times of exceptional inactivity, it cannot entirely cease during life, a fact that distinguishes a living energy-producing organism from dead things.

Respiration, with reference to carbon dioxide, is an excretory function, for in the maintenance of life it seems to be of more importance to get rid of this deadening gas than to acquire more oxygen, although the two processes go hand in hand and are both indispensable. Aquatic animals are easily killed in carbonized water, even when oxygen is present in sufficient amount for breathing. The excretory phase of respiration is clearly demonstrated by the fact that hydrogen sulphide, injected into the blood, is eliminated through the lungs.

Physiologists distinguish between *external* and *internal* respiration. The former is concerned with the gaseous exchange of oxygen and carbon dioxide between blood and air. The latter has to do with the essential transfer between blood and other tissues, or ultimate cells of the body, that constitutes the effective part of respiration, and brings about the release of energy characteristic of life. The distinction between external and internal respiration disappears in small animals which have not elaborated a circulatory system, the transfer of gases taking place directly through the undifferentiated surface of the organism in contact with its atmospheric environment.

3. The Essentials for Any Respiratory Device

In order to utilize the oxygen of the air, any living mechanism that has evolved far enough to have a true circulatory system must meet the fol-

lowing conditions: (1) the blood that is to receive oxygen must be separated from the air by a retaining cellular wall; (2) the wall must be sufficiently permeable to permit easy osmosis of gases; (3) the wall must be kept moist in order to permit thinness and permeability without drying up upon exposure; (4) the total walls or respiratory surfaces must be extensive enough in area to insure an adequate osmosis of oxygen for the organism concerned; and (5) a current of fresh air must be made to pass repeatedly or continuously across the respiratory surface. These conditions are met in a variety of ways by different animals.

4. Different Kinds of Respiratory Mechanisms

In the more primitive aquatic forms, diffuse breathing through the surface of the body precedes localized breathing through specific respiratory organs, such as gills or lungs, although both methods may be employed simultaneously, as in amphibians. Diffuse breathing is a decided handicap, however, since the necessarily delicate integument in animals that employ this method is not only subject to mechanical injuries, but its possessor must remain under water in order to escape the disastrous effects of exposure to drying air.

The two most successful breathing mechanisms among terrestrial animals are *tracheal tubes* and *lungs*. Tracheal tubes, which have been elaborated by the great specialized host of insects, consist essentially of ramifying tubes of intumed integument that admit air to the immediate neighborhood of the blood within the body cavity (Fig. 315).

Lungs are air sacs in intimate proximity to vascular networks, with elaborate modifications for increasing the respiratory surface without harmful exposure to the desiccating effects of the outside air.

In addition to the gills, skin, and lungs of vertebrates, the tracheal tubes of insects, and the more primitive ectoplasmic devices of protozoans, a museum of respiratory inventions would be bound to contain a long array of devices that different members of the animal kingdom use in solving the universal biological problem of gas exchange. To cite only a few of the more familiar of these devices among invertebrates there may be mentioned the *aboral tentacles* of starfishes; the *respiratory tree* safe within the digestive cavity of the mud-inhabiting sea cucumbers; the curious *respiratory bladder* of rotifers; the *integument* of the sinuously waving annelids; the



Fig. 315. Respiratory tracheal tubes of a honey bee. (After Hertwig.)

expansive *mantle* of mollusks; and the compact *lung-books* of spiders. Among vertebrates may be added the remarkable *respiratory tail* of the goggle-eyed *Periophthalmus* of the Indo-Pacific mangrove swamps, a fish



Fig. 316. Branching respiratory barbules of the larva of an African toad, *Xenopus*. (After Bles.)

that can remain for hours out on land with only its highly vascular tail submerged in water. Finally there is an Antillean frog, *Hylodes martinensis*, which undergoes its entire metamorphosis within the egg, likewise accomplishing breathing during this critical period by means of a broad respiratory allantois-like tail.

It must not be forgotten, moreover, that in all reptiles, birds, and mammals, the *allantois* is provided as a temporary breathing organ during embryonic life. This highly vascular device for gas exchange is absorbed before hatching in the case of reptiles and birds, and in mammals is lost at birth with the placenta.

The lungless salamanders which swallow air have a *pharyngo-esophageal network* that acts as an accessory respiratory contrivance to supplement the integument and gills, while the larva of the South American toad *Xenopus* (Fig. 316), possesses a kind of *integumentary chin whiskers* which, according to Bles, are respiratory in function.

Certain fishes, *Callichthys*, *Hypostomus*, *Doras*, *Misgurnus*, and *Cobitis*, breathe by means of a *vascular rectum*, alternately sucking in and squirting out water through the anus. Turtles in similar fashion utilize a pair of lateral *cloacal sacs* with capillary walls.

The air-breathing labyrinthine fishes, *Polycanthus*, *Osphromenus*, *Trichogaster*, *Macropodus*, *Ophiocephalus*, *Clarias*, and the East Indian climbing perch, *Anabas* (Fig. 317), have a peculiar enlargement of the gill cavity, behind the eyes and dorsal to the first and second gill arches, in which pocket-like space there is a much folded vascular structure, the *labyrinth*, that meets all the requirements of a respiratory organ, under the difficult conditions of enveloping mud.

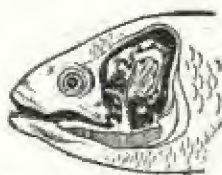


Fig. 317. The gills of the climbing perch, *Anabas*, exposed to show how they are protected beneath the operculum so as to be kept from drying up during the excursions out of water which this curious fish makes. (After Hilzheimer.)

The glimmering flying fishes, *Exocoetes*, that enliven the surface of tropical waters, may "hold their breath" for the brief intervals during which they forsake the water, since their gills do not seem to be supplemented by any peculiar additional breathing organs, although moist gills for a brief time in air would be admirable breathing organs.

The *swim bladder* of fishes, as well as the accessory *air sacs* of birds and of some reptiles, which will be more fully described later, are both special devices connected with the function of respiration.

II. GILLS

The problematical ancestral vertebrates, amphioxus and the tunicates, that are largely sedentary in habit, obtain their microscopic food through ciliary action by creating a current of water which flows into the mouth. Since the current of water also contains oxygen essential to respiration, it is obvious that respiratory organs placed in its pathway will be most favorably located for obtaining oxygen. Gills, lungs, and even more uncommon respiratory devices, such as swim bladders in fishes and pharyngoesophageal capillaries in lungless salamanders, therefore, are found colonizing at the anterior end of the alimentary canal. There is in fact an intimate relationship between the respiratory organs of vertebrates and the anterior end of the digestive tube.

Originally perhaps the entire digestive tube shared in the respiratory function, as suggested in the rectal breathing of certain fishes. Surely in amphioxus as much as the anterior half of the tube is concerned with respiration (Fig. 13). In most vertebrates, however, the apparatus for breathing is more restricted, although still closely connected with the pharyngeal region.

Aquatic vertebrates like fishes have a series of paired lateral openings, the *gill slits*, in the sides of the pharynx, making possible a dual disposal of the water taken into the mouth. This can either pass straight on through the esophagus to the stomach and intestine, in which case its food content is utilized, or it can stream out through the porthole-like gill slits, when the oxygen that it contains is transferred to the delicate respiratory *gills*, or *branchiae*, hanging suspended within the space of the gill slits. In this way both respiration and alimentation are effected.

Between the gill slits, embedded in the walls of the pharynx, are skeletal parts of the splanchnocranium that form the *gill arches*, which furnish support for the vascular gills.

During the early embryonic development of all vertebrates, a series of internal pockets, or *pharyngeal pouches* (Fig. 318A), push outward from the sides of the pharynx. These are lined with the same sort of endodermal tissue found throughout the alimentary canal.

Meanwhile on the outside, corresponding indentations or depressions in the ectoderm, called *visceral furrows* (Fig. 318A), make an appearance.

Later the pouches and the furrows meet, separated only by a thin sheet of tissue which in fishes breaks through to form the *visceral clefts*, or *gill slits* (Fig. 318c), thus completing the passage-way from the pharyngeal cavity to the outside.

In addition, along the margins of the clefts, delicate thin-walled evaginations containing capillaries develop as *gill filaments*, which are the essential organs of respiration. Each *gill septum*, or wall between successive visceral clefts, together with all of the filaments on both of its surfaces makes up a *holobranch*, or *gill*.

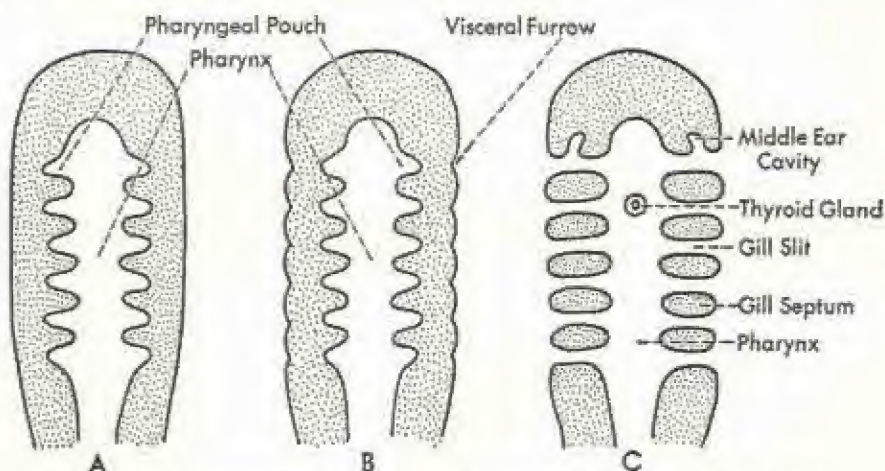


Fig. 318. Diagrams to illustrate the formation of the gill slits. a, early stage showing the outpocketings of the pharynx that form the pharyngeal pouches; a, intermediate stage, showing formation of visceral furrows by inpushings of the ectoderm; c, later stage, in which pouches and furrows have met and formed passage-ways, or gill slits, from the pharynx to the outside. (After Hyman.)

The number of pairs of gill slits varies from fourteen in the cyclostome *Bdellostoma polytrema* of the Pacific Coast, to only one pair, between the third and fourth gill arches, in certain salamanders.

The complicated branchial basketwork of tunicates (Fig. 10) forms a remarkable exception, as well as the sixty or more pairs of gill slits in the elongated pharynx of amphioxus (Fig. 13).

Among reptiles, birds, and mammals gill slits do not normally break through, although both pouches and furrows occur in the embryo. Whenever a pharyngeal fistula, as occasionally reported in medical literature, turns up in a human being, the comparative anatomist, if not himself the possessor of the strange anomaly, is delighted with this reminder of past history.

1. Invertebrate Gills

The gills of invertebrates are not associated with pharyngeal gill slits, as in vertebrates, for there are no gill slits present. Gills may be located anywhere along the outside of the body within easy access of the water. For example, in free-swimming annelids, such as *Nereis*, large leaflike parapodial appendages extending along either side of the body function as "gills." In mud-dwelling or tube-inhabiting annelids gills when present crowd together in beautiful feathery tufts at the exposed anterior end, since they would be at a disadvantage buried within the tube or the mud burrow.

The ciliary "gills" of lamellibranch mollusks are concerned primarily with directing a stream of microscopic food toward the mouth opening, and they are of doubtful respiratory service, this function being performed instead by the expanded surface of the "mantle."

The *thoracic gills* of crustaceans and the *abdominal gills* of larval aquatic insects are simply thin feathery expansions of the chitinous exoskeleton, enclosing tracheal tubes which in this way extend outside of the body rather than being turned inside, as in land tracheates.

2. Primitive Gills of Amphioxus and Tunicates

The fact that tunicates are enveloped in a thick non-respiratory cellulose tunic makes necessary an enlarged pharyngeal basket, that forms a respiratory structure often exceeding in size all the other organs of the body. The tunicate *Phallusia* (Fig. 10), for example, has a branchial basket perforated with several hundred gill slits, while the ghostly transparent Appendicularia, which are microscopic tunicates without a cellulose mantle and consequently with greater capacity for diffuse integumental breathing, possess only a single pair of gill slits.

Amphioxus is characterized by an exceptionally generous number of gill slits, and these are bordered by flat primitive vascular tissue that presents much less respiratory surface than is common to the more elaborate gills of fishes and amphibians. No expansive gill filaments, such as appear in higher aquatic vertebrates, are found hanging in the gill slits, so this ancestral animal is obliged to make up in number what it lacks in area of individual gills. The entire pharyngeal region is enclosed in an *atrial cavity*, so that the pharynx opens indirectly to the outside through a single ventral *atrial pore*, instead of directly through the gill slits. The walls of this atrial chamber protect the delicate gill surfaces from the sand in which amphioxus burrows, while allowing the unobstructed passage of water through the gill slits.

Since the numerous gill slits of both amphioxus and the tunicates increase the hazard of the escape of food through them, the development of a device for directing bits of food past these lateral openings to the



Fig. 319. Diagrammatic cross section through the endostyle of *Clavelina*, showing glandular walls and ciliary bands in the groove. (After Seeliger.)

esophagus is necessary. The apparatus accomplishing this end consists of two ciliated glandular grooves, the ventral *endostyle* (Fig. 319), and the dorsal *epibranchial groove*, in which food particles become collected together into a sort of mucous rope that spins along continuously into the gullet. Later in vertebrate evolution, when the endostyle is no longer needed for the purpose of collecting and steering food, this pharyngeal groove becomes transformed into the *thyroid gland* with an entirely different function.

The student of comparative anatomy often finds things like this in the morphological junk pile, that have become utilized for purposes entirely different from those to which they were originally put.

3. Cyclostome Gills

The arrangement of gills in cyclostomes is somewhat different from that in typical fishes. In *Petromyzon* a forward extension of the esophagus forms a partition between the alimentary and respiratory parts of the pharynx, leaving the branchial apparatus in a blind pocket ventral to the esophagus (Fig. 320). Water in its passage over the gills consequently may enter through the anterior gill slits instead of the mouth, which is frequently otherwise occupied on account of the suction habits of these animals. The gill slits are also modified by the narrowing of each end of the visceral cleft so that the filaments are enclosed in a rounded sac with a slender duct leading to it from the pharynx and another from it to the surface of the body (Fig. 321). Since the gills are located in these pockets, cyclostomes are frequently referred to as *Marsipobranchs*, meaning "pouched gills." In this group different species of *Bdellostoma* have from ten to fourteen pairs of gill slits; *Petromyzon*, eight embryonic pairs but only

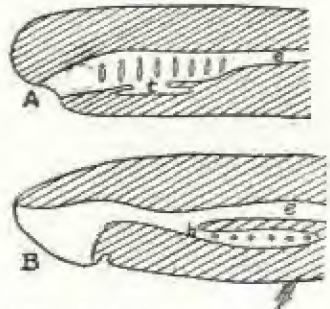


Fig. 320. Diagram of the relation of the esophagus and respiratory tract in (A) *Myxine* and in (B) *Petromyzon*. *b*, branchial duct; *e*, esophagus; *t*, thyroid gland. (After Kingsley.)

seven in the adult; and *Myxine*, six pairs, with all the external passage-ways on each side of the body uniting into a common canal opening by a single pore to the outside (Fig. 321B).

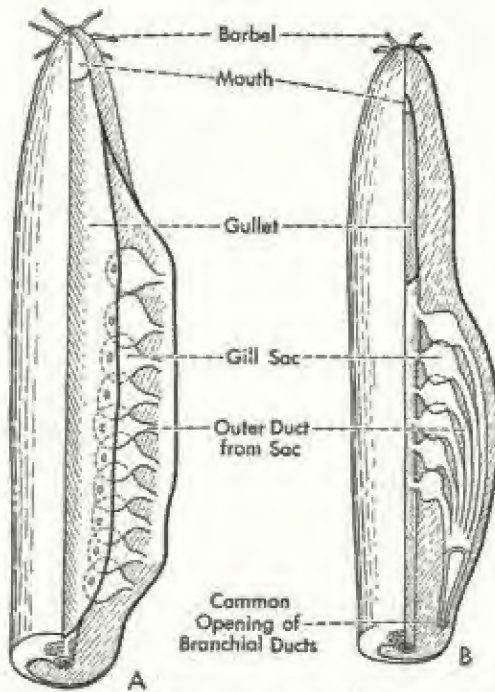


Fig. 321. Diagrams of the heads of (A) *Bdellostoma* and (B) *Myxine*. Dorsal views partly dissected to show arrangement of gills. (After Dean.)

4. Elasmobranch and Holocephalan Gills

Gills of elasmobranch fishes are lateral in position in sharks and dogfishes but ventral in the flattened skates and rays. They open independently to the outside and are separated from each other not only by skeletal gill arches of cartilage, but also by primitive partitions attached to these arches, called *branchial septa*, on either side of which is located a set of filaments, or *demibranch*. A septum and its two demibranchs together make up a *gill*, or *holobranch*. Along the inner margins of the gill arches are finger-like projections, the *gill rakers*, which not only keep food from entering the slits but also aid in directing it along the straight and narrow esophageal path in which it should go (Fig. 322A).

The most anterior pair of the pharyngeal portholes in elasmobranchs, between the mandibular and the hyoid arches, develops into the *spiracles*,

not far posterior to the eyes in position. The walls of the spiracles are not provided with true gills, but in some cases may support, on one side at least, a "false gill," or *pseudobranch*, so called because its blood supply is not derived directly like that of true gills from an afferent branchial artery bearing "impure" blood, but from the efferent branchial artery of the following gill arch which, having already given up its load of carbon dioxide and taken in oxygen, carries "pure" blood.

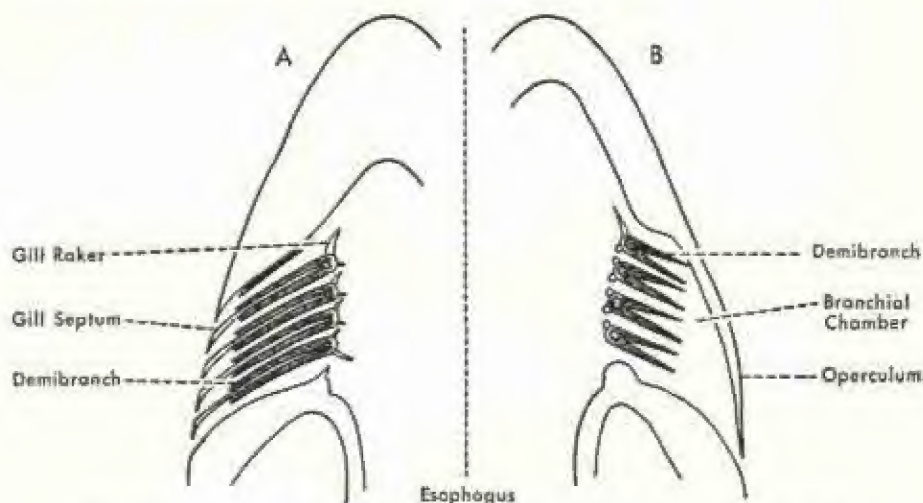


Fig. 322. Relation of gills to branchial chamber. A, elasmobranch, with long gill septa; B, teleost, without gill septa. (After Schimkewitsch.)

In bottom-feeding skates and rays the spiracles open dorsally instead of ventrally as the other pharyngeal gill slits do. They are useful, therefore, in taking the water of respiration into the branchial cavity when the mouth is otherwise occupied grubbing for food in the mud. No doubt sharks and dogfishes, which swim about freely and gracefully in water, likewise use the spiracles upon occasion, instead of the mouth, as an accessory port of entry for the water of respiration. The cub shark, *Carcharias*, and the mackerel shark, *Lamna*, are without spiracles.

The primitive shark, *Heptanchus*, has seven pairs of gill slits, and the frilled shark, *Chlamydoselachus*, as well as *Hexanchus*, six pairs, while for most elasmobranchs the typical number, aside from the spiracles, is five pairs. On each face of each gill slit, except the posterior side of the last slit, there is a demibranch, making a total of nine pairs of demibranchs in a fish with five pairs of slits.

Certain larval elasmobranchs which undergo considerable development within the eggshell before hatching have gill filaments so long that they hang out of the gill slits as temporary "external gills" (Fig. 323). These unusual structures may serve not only for respiration but also as absorbing organs in connection with the enormous yolks present in these eggs.



Fig. 323. Embryonic "external gills" of dogfish. (After Schimkewitch.)

The holocephalans, or strange elephant fishes, which have much in common with elasmobranchs, possess only four pairs of gill slits and are further differentiated from them by an *operculum*. This is a flap of the integument developed on either side and extending backward from the margin of the hyoid arch, until it covers the external openings of the three anterior pairs of gill slits, leaving only the last pair open directly to the outside after the elasmobranch fashion. Possibly the forerunner of this opercular flap is seen in the elasmobranch, *Chlamydoselachus*, where the skin on the anterior margin of each gill slit extends backward as a small independent protective fold covering the opening of each gill slit separately (Fig. 324), a feature which gives *Chlamydoselachus* the common name of "frilled shark."



Fig. 324. A primitive shark, *Chlamydoselachus*, with an external flap for each separate gill slit. (After Schimkewitch.)

5. Ganoid and Teleost Gills

The gill system of ganoids in some ways represents a connecting link between that of elasmobranchs and teleost fishes. Most Chondrostei still have nine pairs of demibranchs but nearly all Holostei lose the most anterior pair so that they are limited to eight pairs of demibranchs, i.e., four pairs of complete gills. In all bony fishes the gills are covered by an operculum that is stiffened by flat skeletal plates between the two surfaces of folded integument. Outside and anterior to the operculum on either side, there is a degenerate spiracle in some of the ganoids, while on the inner surface of the operculum there is attached a small *opercular gill* which is not homologous either with true gills or with the pseudobranchs of the hyoid arch.

The interbranchial septa in ganoids are reduced so that the demibranchs placed upon them back to back are no longer in separate individual chambers, but occupy a common branchial cavity (Fig. 325c). The reduction of the interbranchial septa becomes complete in teleost fishes, so that the gills all lie compacted closely together in a common chamber covered by the operculum (Figs. 322b and 325e).

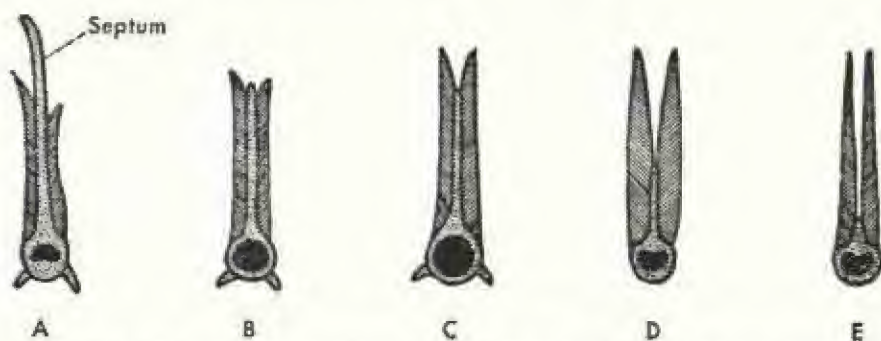


Fig. 325. The progressive reduction of gill septa in different fishes. A, elasmobranch; B, holocephalan; C, ganoid; D and E, teleosts. (After Boas.)

The number of gill arches in both ganoids and teleosts is usually four or five pairs, although they may be reduced to three, or even two pairs in some of the bony fishes. Spiracles are not characteristic of teleosts.

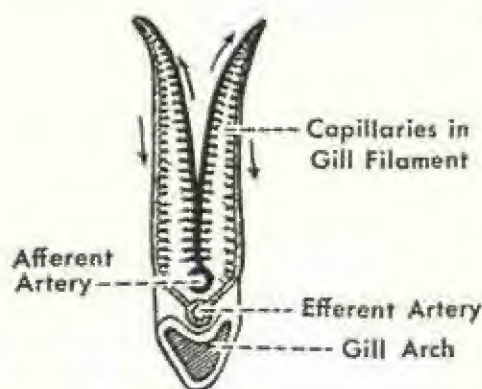


Fig. 326. Structure of a typical gill, showing blood vessels. (After Cuvier.)

The opercular opening becomes much diminished in such fishes as eels, which are thus enabled to retain water in the branchial chamber under unfavorable conditions. Probably the immediate reason why fishes suffocate when removed from a water environment is not because the gills dry up at once with a collapse of the capillaries in the gill filaments, but because when out of water the gills adhere to each other, leaving the exposible respiratory surface reduced beyond the danger point.

The structure of a typical teleost gill, with its relatively great expanse of respiratory surface within a small compass, and the arrangement of its capillaries are indicated in Fig. 326.

In ganoids and teleosts there are additional devices, besides the opercular lid, for protecting the delicate gills. Along the posterior and ventral margins of the operculum beyond the part stiffened by the flat opercular bones, a bordering fringelike flap is sometimes developed, which is supported by fanlike skeletal elements, the *branchiostegal rays*, that help in controlling the passage of water out of the branchial cavity.

On the inner pharyngeal side of the gill slits also there are present in varying degree, a series of stiff comblike projections along the inner margins of the gill arches, the *gill rakers*.



Fig. 327. External gills in a larval stage of *Lepidosiren*. (Alter Kerr.)

6. Dipnoan Gills

Of the three genera of living lungfishes that are found respectively in Australia, South America, and Africa, *Neoceratodus* has four pairs of gills, *Lepidosiren*, three, and *Protopterus*, two. Spiracles are present in the embryos of these fishes, although not in the adults. In addition to the pharyngeal gills common to this group, four pairs of supplemental *true external gills* of the pinnate (*pinna*, feather) type are present in the larval stages of *Lepidosiren* and *Protopterus* (Fig. 327).

7. Amphibian Gills

The external gills of amphibians are attached as capillary detours upon the aortic loops in such a way that blood can go either directly around the vascular loops or round-about through the gills (Fig. 328). This is quite different from the arrangement of the internal gills of fishes, which offers no alternative for the circulating blood except to pass through the gills themselves.

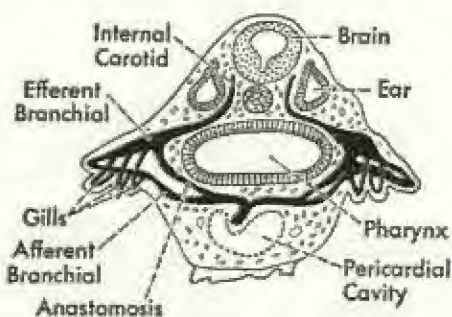


Fig. 328. Section through branchial region of a 6 mm larva of *Rana esculenta*, showing vascular loop, in external gills and anastomosis between afferent and efferent branchial arteries. (After Maurer.)

As compared with internal gills, external gills are only weakly supported by a skeletal framework, and although always present during the tadpole stages of amphibians, they persist throughout life only in the perennibranchiate urodeles, as the name indicates. Such external gills occur in the larval forms of a few fishes, for example, in the dipnoans as already mentioned, in the cartilaginous ganoids, *Polypterus* and *Calamoichthys*, and in the teleosts, *Gymnarchus* and *Heterotis*.

The urodele amphibians have been separated into three groups according to the character of their gills, as follows: (1) *Perennibranchiata*, retaining both gills and gill slits throughout life; (2) *Derotremata*, losing gills and all the gill slits except one pair; and (3) *Myctodera*, or true salamanders, having neither gills nor gill slits when adult.

Although perennibranchiates preserve throughout life their tadpole-like external gills with two or three pairs of gill slits, these pharyngeal openings are no longer useful for their original purpose, since the water of respiration does not pass through the pharynx. Instead a fresh supply of dissolved oxygen is brought into contact with the gill filaments as the gills wave to and fro in the water, by means of muscles attached to the base of each gill. Five pairs of gill pouches form embryonically in the pharyngeal cavity, but the first and the fifth no longer break through. *Necturus* and *Proteus* belong in this group.

In derotremes only the gill slit between the third and the fourth gill arches becomes complete, while the external gills vanish during larval life.

Amphiuma, *Cryptobranchus*, and *Siren* are derotremes.

The myctodere salamanders, as well as frogs and toads, have no gill slits, although embryonic pouches and furrows develop. The temporary external gills of these forms are sacrificed with the development of pulmonary and cutaneous respiration. The newts and true salamanders, including *Amblystoma* and *Triton*, are myctoderes.



Fig. 329. External leaflike gills of a larval caecilian. (After P. & F. Sarasin.)

The external gills of frog tadpoles become enclosed during metamorphosis by a fold of the skin without skeletal support, while the protective peribranchial chamber thus formed usually has a single opening to the outside, more rarely two, as in *Pipa* and

Xenopus, corresponding physiologically to the atrial pore in the peribranchial chamber of amphioxus (Fig. 13).

One of the tropical limbless amphibians, *Caecilia*, is exceptional, having larval external gills of peculiar crumpled leaflike structure, with a relatively large respiratory surface (Fig. 329).

8. Gill Structures in Land Vertebrates

The persistence of branchial remains in land forms, that have no use for gills even in embryonic life, is striking evidence of the common ancestry of all vertebrates.

Although gills are never present in reptiles, birds, or mammals, there are five pairs of embryonic visceral pouches and furrows in reptiles and mammals and four pairs in birds. Ordinarily these break through only briefly in reptiles and birds but not at all in most mammals. Only the anteriormost, or hyomandibular, pair remains well developed in adult mammals. The hyomandibular pouches become the *Eustachian tubes* and the *middle ear cavity*, which ordinarily remain separated by the *ear drum* from the *external ear canal*, derived from the ectodermal furrows (Fig. 692).

III. SWIM BLADDER

A *swim bladder*, or *air bladder*, is found in most fishes. It is a derivative of the anterior region of the digestive tube and, if not primarily respiratory in function, is at least found in suspicious intimacy with respiratory organs.

Located dorsally in the body cavity just outside of the peritoneum under the vertebral column (Fig. 330), it is ordinarily a single elongated structure, although it may be bifurcated or paired, as for example in *Polypterus*

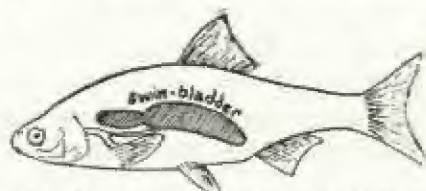


Fig. 330. Location of the swim bladder. (After Hesse.)

and *Calamoichthys* among ganoids and in the swellfish, *Sphaeroides*, the curious headfish, *Mola*, and the sea robin, *Prionotus*, among teleosts.

Great variation in the shape, form, and size of the swim bladder is connected with its hydrostatic function, as well as with variation in the center of gravity in different shaped fishes.

In amphioxus, cyclostomes, elasmobranchs and a few of the higher fishes, particularly bottom-feeders and deep-sea forms, the swim bladder is absent. The flatfishes (Pleuronectidae) possess a swim bladder only in early life during the period when they maintain a vertical position. As they tip

over on one side in the course of development and assume their lazy adult habit of life, the swim bladder degenerates.

Fishes which possess swim bladders in the adult form may be divided into two groups according to the character of the swim bladder, namely, the *PEYSOSTOMI*, having a *pneumatic duct* leading from the swim bladder to the alimentary tract; and the *PHYSOCLISTI*, having the outlet duct closed or atrophied. To the first group belong the bony ganoids, the dipnoans, and the soft-rayed teleosts. In the latter group are included all the spiny-rayed fishes.

The pickerel, *Esox*, represents a simple type of physostomous fish having a single sac for a swim bladder, with a pneumatic duct at the anterior end opening into the esophagus (Fig. 331A). In some fishes the single swim bladder is made up of two connecting sacs (Fig. 331B).



Fig. 331. Diagrams of swim bladders. The eel shows the posterior chamber forming by the enlargement of the pneumatic duct. (After Tracy.)

In physoclistous fishes, upon the degeneration of the pneumatic duct, the swim bladder becomes a closed sac having two chambers separated by a partition through which there is a sphincter-like opening, regulated in size by both circular and radiating muscles similar in arrangement to those in the iris of the eye. The *posterior chamber* is formed by an enlargement of the pneumatic duct that is no longer needed for its original function. This is quite apparent in the eel, *Anguilla*, a physostomous fish on the verge of becoming physoclistous, in which the duct is caught in the very act of enlargement into a separate chamber (Fig. 331C). The formation of the posterior chamber by the enlargement of the pneumatic duct has been clearly indicated by Tracy in a series of diagrams based upon wax reconstructions of serial sections, showing stages in the development of the swim bladder in the pipefish, *Siphostoma* (Fig. 332). The manner in which the *anterior chamber* is produced by the forward growth of the budding swim bladder has also been demonstrated by Tracy in the early stages of the toadfish, *Opsanus* (Fig. 333), which later develops a typical closed swim bladder, with the same three histological layers of tissue that characterize the

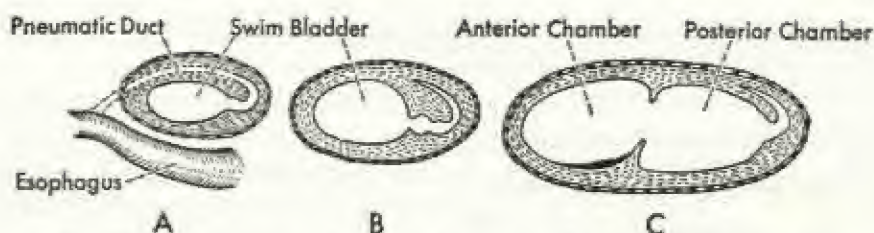


Fig. 332. Diagrams to show the formation of the posterior chamber of the swim bladder from the pneumatic duct in the pipefish, *Siphonotoma*. A, at the time of the release of the larva from the brood sac; B, stump of pneumatic duct growing backward to form U-shaped tube; C, pneumatic duct expanded to form posterior chamber. (After Tracy.)

alimentary tract from which it was derived, shown in section in Figure 333F.

An important modification in the epithelial lining of the anterior chamber of the swim bladder results in a structure unique among animal tissues, the *red gland*, which produces free oxygen (O_2) by the reduction of oxyhaemoglobin in the red blood corpuscles when brought into close contact with secreting epithelial cells. No other gland is capable of isolating pure molecular oxygen. As Tower has demonstrated, this oxygen constitutes a large part of the gas that distends the swim bladder.

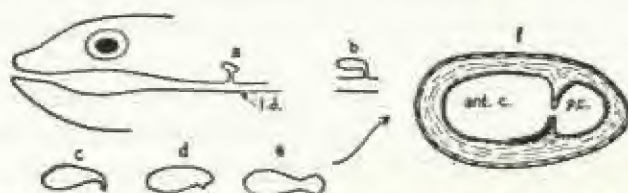


Fig. 333. Diagrams of the early stages in the formation of the closed swim bladder in the toadfish, *Opsanus l.d.*, liver duct; ant.c., anterior chamber; p.c., posterior chamber. (After Tracy.)

Excess gas produced by the red gland escapes through the pneumatic duct in all physostomous fishes. Since the two-chambered swim bladders of physoclistous fishes have the red gland located in the anterior chamber, the mechanism for the removal of excess gas is of necessity different from that in fishes with a pneumatic duct. The entire posterior chamber is lined with a thin epithelium beneath which is a capillary network, the *rete mirabile*, through which excess gas generated in the red gland is absorbed directly into the blood. By enlarging the opening in the partition between the chambers, more gas is admitted to the posterior chamber for disposal through the blood, while by restricting it, the gas is retained. In this way the degree of

distention of the swim bladder is automatically regulated by the interaction of the red gland and the rete mirabile.

A further modification of the closed swim bladder sometimes appears, for example in the squeteague, *Cynoscion* (Fig. 334), when the posterior

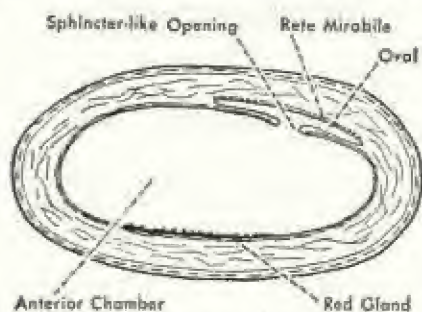


Fig. 334. Closed swim bladder of squeteague, *Cynoscion*, showing oval, the reduced posterior chamber. (After Tracy.)

chamber with the rete mirabile becomes flattened almost to obliteration and is designated as the *oval*.

There are various uses for the swim bladder in fishes. Although primarily respiratory, it has become in most instances a *hydrostatic organ*, or "float," for the purpose of maintaining a certain level in water without muscular effort. When its gaseous content is increased, the fish rises to higher levels, or if diminished, sinks deeper in the water.

By shifting the volume of gas from one end of the swim bladder to the other through muscular compression, changes in the center of balance in the body also occur, which enable the fish to make a variety of movements easily at the same level.

In some fishes, particularly Siluroids, Cyprinoids, and Gymnoti, anterior prolongations of the swim bladder are present that come into intimate relation with the inner ear either directly or through a chain of bones derived from parts of the first three vertebrae, forming the so-called *Weber's organ*. Variations in the distention of the swim bladder are conveyed to the inner ear by means of this device, that probably acts as a regulatory sense organ either after the fashion of a manometer or a barometer. Whether Weber's organ aids in any way as an organ of hearing is doubtful.

Another use for the swim bladder is that of *respiration*, for which reason its description is included in the present chapter. This function applies particularly to lungfishes, whose swim bladder becomes alveolar inside like the lungs of amphibians and the lower reptiles, being usually paired as well as taking on all the essential features of simple lungs. It even derives, after the fashion of true lungs, a supply of venous blood from the last pair of aortic loops, whereas the typical hydrostatic swim bladder receives arterial blood only, and gives off venous blood. The swim bladder of lungfishes, therefore, apparently is a more efficient breathing organ than the primitive lungs of the perennibranchiate urodeles.

A third incidental use of the swim bladder is the *production of sound*. Drum fishes (*Sciaenidae*), "grunters" (*Haemulonidae*), and a few other

forms, such as the sea-robin, *Prionotus*, and the toadfish, *Opsanus*, are exceptional noise-producers in a modest way among the otherwise mostly silent brotherhood of fishes. According to Tower, who has carefully investigated the matter, the chief source of the drumming noise in drum fishes is the contraction of a "drumming muscle," *musculus sonificus* (Fig. 335), which, being superficially attached to the swim bladder, "produces a vibration of the abdominal walls and organs, and especially of the swim bladder." D. S. Jordan says that the "grunting" of the Haemulonidae is caused "by forcing air from part to part of the complex swim bladder."

IV. LUNGS

1. General Plan

Lungs are the typical breathing organs of the higher vertebrates. *Physiologically* they represent an apparatus interposed between the two parts of a double heart and in which air and blood are brought together. *Morphologically* they consist of a much elaborated respiratory surface of maximum exposure within a minimum space, together with a system of non-collapsible passage-ways for admitting air from the outside, that passes over these respiratory surfaces in intimate juxtaposition with capillaries.

The passage-ways to the lungs begin either with the *nasal chamber* or *oral cavity*, leading through the *pharynx* to the *trachea*, *bronchi*, and *bronchioles*, and eventually reaching the innumerable terminal *alveolar sacs* that constitute the true respiratory area where the gaseous exchange of respiration is effected.

Gills have one place for the intake of the oxygen-containing water (the mouth) and another for the outgo (gill slits), so that the respiratory procession is continuous. In animals with lungs the same part is employed for the entry and departure of oxygen-containing air, with the result that inspiration and expiration become alternating processes.

It is estimated that in man the respiratory alveolar surface enmeshed in

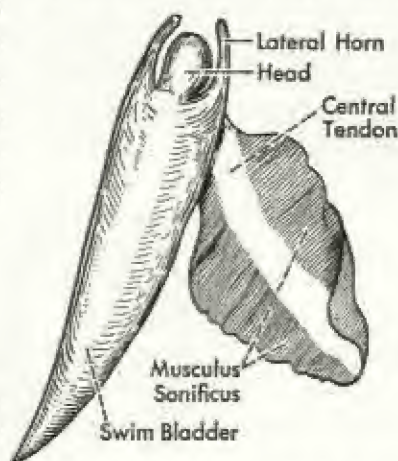


Fig. 335. Swim bladder of male squeteague, *Cynoscion*. The double *musculus sonificus* is shown laterally displaced. The central tendon of the *musculus sonificus* lies free in the mid-dorsal line just above the swim bladder and below the kidneys. The double *musculus sonificus* is inserted laterally in the common fascia of the rectus abdominis muscle, and by its contraction in connection with the distended swim bladder gives rise to the drumming sound. (After Tracy.)

capillaries makes a total expanse of a hundred times the area of the entire skin, or, if inflated into a single sac, one that would form a balloon ten feet in diameter, yet this extensive structure is packed away in a relatively small space, the contour of which is determined largely by neighboring organs and general form of the body.

Alveoli in contact with capillaries are lined with thin pavement epithelium, but the trachea, bronchi, and in part the bronchioles leading to the alveoli, are lined with ciliated cells, the activity of which, so long as they remain moist, tends to keep the air passages free from dust and other foreign intrusions.

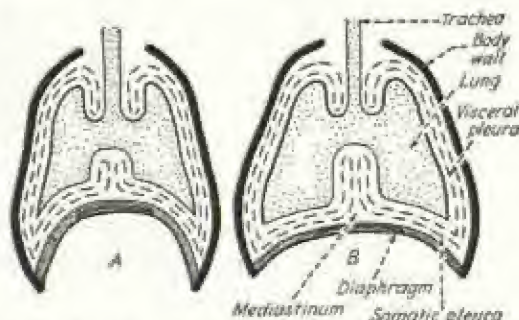


Fig. 336. The lungs in the thoracic cavity. A, air expired by raised diaphragm and compressed ribs; B, air drawn in by lowered diaphragm and expanded ribs.

The lungs as a whole are highly elastic and, although encapsuled in a double pleural sac in the higher vertebrates, are freely movable within the sac, except at the point of their attachment near the base of the bronchi (Fig. 336). Here they are joined by the trachea, a stalklike tube connecting with the pharynx, and are penetrated by the pulmonary artery and vein which hook up with the heart and the circulatory apparatus. Otherwise the lungs are free and unattached, thus enabling them to glide easily over the inner surface of the thorax with every breath while filling all the available spaces.

The whole apparatus, which somewhat resembles in form a compound sebaceous gland, might be compared to a luxuriant tree, entirely hollow in all its parts, that has been pulled up by the roots and crowded top first into a bag. The root region corresponds to the nasal chamber, the oral cavity, and the pharynx; the main trunk of the tree to the trachea; the larger branches to the bronchi that subdivide into lesser branches and twigs, or bronchioles, terminating in the leafy foliage, or alveoli, that are crowded together in such a way as to occupy all available space within the enveloping sac, or pleural envelope.

2. Air Passages

(a) **Nasal Chamber and Pharynx.**—The entrance to the pulmonary system is usually through the air-conditioning *nasal chamber* (Fig. 252), although in higher vertebrates the oral cavity may also serve in an emergency as an entrance. The nasal chamber is lined with a mucous membrane, known as the *Schneiderian membrane*. The tissue beneath this lining layer is richly supplied with capillaries, thus providing moisture and a certain degree of warmth for incoming air. A moistened surface is further insured by the fact that the lacrimal ducts, from the constantly operating *tear glands* in the bony orbits of the eyes, drain into this chamber. The ciliated cells of the Schneiderian membrane maintain a continuous flow of mucus, and adhering particles of foreign matter, from the nasal cavity into the oropharynx.

The walls of the nasal chamber are variously enlarged in different vertebrates by scroll-like *turbinate bones*, which not only increase the moist vascular surface, but also prevent an easy entrance of undesirable objects by making the passage-way tortuous. This latter purpose is also furthered by a forest, more or less dense, of outward-projecting hairs guarding the entrances, or nostrils, of the nasal chambers. This part of the air passages is cleared of undesirable accumulations by "blowing the nose." Man is the only mammal that performs this feat in any way acceptable to his neighbors.

(b) **Trachea.**—From the nasal cavity air passes back through the *nasopharynx* to the *oropharynx*, where it crosses the food route on the way to the esophagus, thence entering the trachea through a slit-like opening, the *glottis*.

The trachea, or "windpipe," is a rigid tube, very short in frogs and toads whose lungs are far anterior in the body cavity. It is somewhat longer but still insignificant in the urodeles. In lizards it is relatively shorter than in other reptiles, although unmistakably present, while in turtles and crocodiles it is frequently so long that it becomes convoluted or even spiral in form. The lengthened trachea in the chelonians is an accommodation to the accordion-like movements of the head and neck.

Birds with long necks are of course provided with a long trachea, but frequently the trachea is even longer than the neck itself, so that it cannot remain straight but loops about. In swans these extra loops are stored within the hollow breastbone (Fig. 337), while in some birds they lie coiled under the skin, or may even extend into the body cavity. Extra long tracheae make it possible for their possessors to stretch out the neck without pulling the lungs out "by the roots."

Usually the windpipe is nearly cylindrical, but sometimes, as in the little vocal wall lizards, or "geckos," and also certain ducks, it may show a bulb-like enlargement that acts as a resonance sac when air is expelled.

In mammals the trachea is practically straight, with a length directly dependent upon that of the neck; except in the three-toed sloth, *Bradypus*, whose trachea is so elongated that it extends down as far as the diaphragm and back before entering the lungs. It will be remembered that the upside-down sloth, while hanging from the limbs of tropical trees, feeds lazily upon leaves without scrambling about. It therefore has a very stretchable neck.

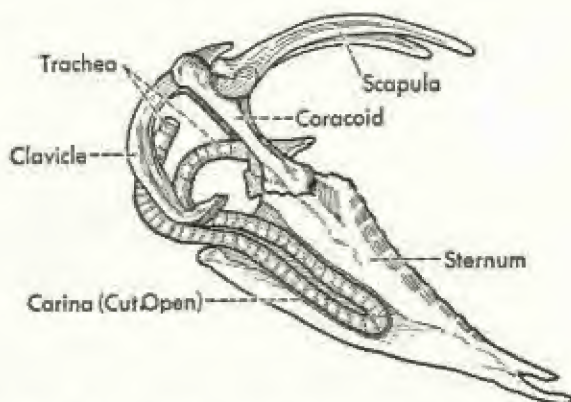


Fig. 337. Trachea of swan, embedded in sternum. (After Schimkewitsch.)

At all times the elastic walls of the trachea are kept mechanically distended for the passage of air by encircling rings of cartilage, resembling the metal rings embedded in a garden hose to give it flexibility and durability, and at the same time to keep it uncollapsed and open. In the case of mammals these skeletal tracheal rings are usually incomplete on the dorsal side, that is, on the side liable to press against the esophagus that lies parallel to it, thus minimizing the "corduroy road" effect that might otherwise be encountered by a bolus of food when swallowed.

Among reptiles, birds, and pinniped mammals, the tracheal rings are entire, while cetaceans present the unusual case of tracheal rings incomplete on the ventral rather than the dorsal side.

Camels and giraffes are noteworthy in having upwards of one hundred separate tracheal rings, and whales and sea-cows in having these skeletal structures spirally arranged.

Although usually of hyaline cartilage, tracheal rings become bony in the python *Agama*, and also in many birds.

(*c*) **Bronchi.**—The trachea usually branches into two bronchi, that resemble it in structure with the exception of being smaller in size and in having weaker skeletal rings.

There are three bronchi in certain ruminants, pigs, and whales, but in most snakes, with the degeneration of one lung as an accommodation to the extraordinarily elongated shape of the body, there remains only one bronchus.

(*d*) **Bronchioles.**—Bronchioles, which continue and multiply the air passages from the bronchi, have only limited cartilaginous supports which are in the form of rings. These supports become progressively smaller, and the mucous cells of the linings of the bronchioles fewer, until both are completely absent from terminal bronchioles. The latter serve simply as ducts leading the way into the ultimate air chambers, or alveoli, in which respiration occurs.

In mammals generally the bronchioles arise like the twigs of a tree and diverge from each other, but in crocodiles and birds they run together, forming intercommunicating loops instead of terminal twigs, from the sides of which alveoli are given off.



Fig. 338. Diagram showing relation of capillary, carrying blood, to alveolus, containing air.

(*e*) **Alveoli.**—The alveolar sacs, or the respiratory part of the whole system of air passage-ways, are hemispherical enlargements at the ends of the bronchioles. They have exceedingly thin delicate highly elastic walls over the outside of which, like vines over a trellis, extends a closely woven maze of capillaries (Fig. 338). It is estimated that in a pair of human lungs there may be more than six million of these tiny chambers, all in ultimate communication with the outside atmosphere through the air-passages which unite in the trachea.

The amount of air admitted to the alveoli is automatically regulated by means of nerve endings, the headquarters of which are located in the medulla of the brain. These nerve endings are inserted into tiny cuffs of circular muscle fibers that encircle the walls of the innumerable bronchioles, causing them to constrict or relax, as occasion demands.

3. Phylogeny

The phylogeny of the lungs is a story of internal modification for the increase and efficiency of the respiratory surface, and also for adaptation to the shape of the body. The storing of lungs, for example, within the body of a squat toad, a lithe cat, a capacious cow, a box turtle, or an elongated snake, presents in each instance a different problem.

(a) **Dipnoans.**—A transition between the swim bladder and true lungs is found in the dipnoans which, although not ancestral to the land vertebrates, show many of the features probably possessed by the ancestors of the latter. During the aestivation of these lungfishes the gills are not used for respiratory purposes, but instead branches of the sixth aortic loops, the pulmonary arteries, bring venous or "impure" blood to the swim bladder,

which then functions as a lung. Pulmonary veins return the blood to the left side of the auricle. *Polyp-terus* and *Amia* are the only other fishes with similar pulmonary arteries but their veins send the blood into the sinus venosus.

In *Neoceratodus*, the lung or swim bladder is a single wide sac, resembling the swim bladder of physostomous fishes, but in *Protopterus* and *Lepidosiren*, the sac is bilobed, its inner surface being increased somewhat by its coarse spongy alveolar structure.

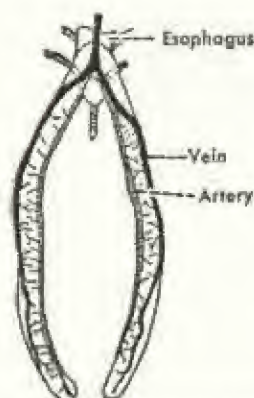


Fig. 339. Ventral view of the lungs of *Necturus*, showing arrangement of blood vessels on them. (After Miller.)

(b) **Amphibians.**—Amphibians in general carry on the pulmonary plan of the dipnoans although the primitive lungs of perennibranchs are less elaborated than those of the lungfishes. The lungs of *Necturus* (Fig. 339), for instance, are two long simple sacs, enmeshed on the outside by arterial and venous capillaries and opening directly through a slitlike glottis without the intervention of either trachea or bronchi. The inner surface is not increased by folds. The whole apparatus, resembling a pair of enlarged elongated alveolar sacs, is probably more hydrostatic than respiratory in function.

Amphiuma goes a step further, in that the proximal half of each lung has the inside surface considerably increased by the elaboration of folds.

Owing to the form of their bodies, frogs and toads have more spherical lungs than salamanders. The folds within the frog's lungs extend from the inner walls in such a way as to divide the entire cavity into marginal stall-like spaces or compartments, all opening freely into a common central

cavity. The double walls of the "stalls," formed by the invagination of the outside wall, each carry a capillary network which increases the available blood supply over the surface of the lungs (Fig. 340). In toads the stalls become partially shut off from the central cavity of the lung by right angle additions along the inner margin of the partition walls, so that a secondary internal wall is formed that is perforated on all sides with openings between the central cavity and the air chambers, or stalls, which resemble semi-private luncheon niches around the margin of a common dining room.

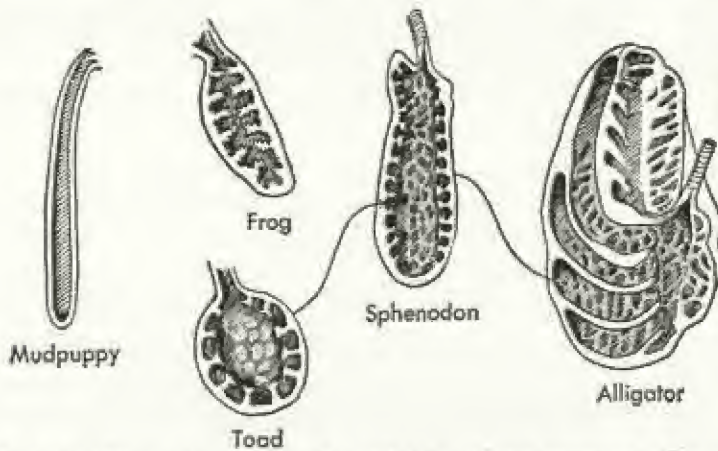


Fig. 340. Diagrams to show the evolution of lung structure. The plan of the lung of *Sphenodon* may be regarded as like a cluster of toads' lungs; in turn the alligator's lung may be considered as composed of several lungs of the *sphenodon* type.

The very primitive tracheal and bronchial tubes of amphibians enter the lungs at the extreme anterior end. With an increased development of the anterior part of the lungs, the bronchi acquire a more lateral entrance in higher forms.

As a result of a migratory invasion into the body cavity, the lungs of amphibians become invested on the outside by a single layer of peritoneum, which is pushed ahead of them into the body cavity during development. They do not, therefore, have a separate pleural cavity of their own, but instead lie freely in a common body cavity.

Usually the left lung in amphibians is larger than the right one, but in tropical legless forms (*Apoda*) the reverse is true, as the left lung is rudimentary. Some salamanders, for example *Eurycea* and *Salamandrina*, are lungless, respiration being accomplished through the integument and the bucco-pharyngeal epithelium.

(c) **Reptiles.**—Integumental breathing is eliminated in reptiles, whose lungs, also abdominal in position, are much sacculated within and whose trachea and bronchi are developed into definite structures. The air-transferring passage-ways and the air-absorbing mechanism of the lungs are distinctly differentiated in reptiles.

The primitive New Zealand lizard, *Sphenodon*, has spongy lungs that might be compared to a cluster of lungs like those of a toad, opening into a common passage, or *atrium* (Fig. 340), while the lungs of crocodiles go a step further in elaboration, corresponding to a bouquet of *Sphenodon* lungs placed together, the atria of which now open into a common bronchus.



Fig. 341. Lungs of *Chameleon*, showing supplementary air sacs. (After Wiedersheim.)

In snakes the left lung usually becomes aborted, only the right lung remaining to occupy the narrow quarters that are available. Boa constrictors and pythons are the most ancestral in this respect, having both lungs present with the left one somewhat shorter than the right.

The different levels of the long single lung of the snake are unequally elaborated, recapitulating from distal tip to the entrance at the glottis the early phylogeny of vertebrate lungs. Thus, the distal tip is a smooth sac like the lung of *Necturus*, but advancing toward the proximal or anterior end there develops a gradual evolution of internal folds, at first resembling the lungs of *Amphiuma*, and later the chambered structure of the lungs of frogs and toads. Finally, at the base, these chambers become compounded and open into an atrium, suggesting the degree of complexity arrived at in the lung of *Sphenodon*.

Certain lizards, particularly *Chameleon* (Fig. 341), have peculiar lungs with saclike diverticula, which enable them to swell up to a certain extent, a device used perhaps to frighten their enemies. The inflated lungs of sea turtles, on the other hand, probably serve as floats, or life preservers, in maintaining a position at the surface of the water.

(d) **Birds.**—The lungs of all modern birds are highly modified by the presence of supplementary *air sacs*, *cellulae aëreae*, which facilitate the circulation of air through the lungs, but in themselves are not directly respiratory in function, as shown by the paucity of capillaries over their surfaces.

The bronchioles, instead of ending blindly in alveolar sacs, form a system of communicating loops, and open eventually into the reservoir-like air sacs

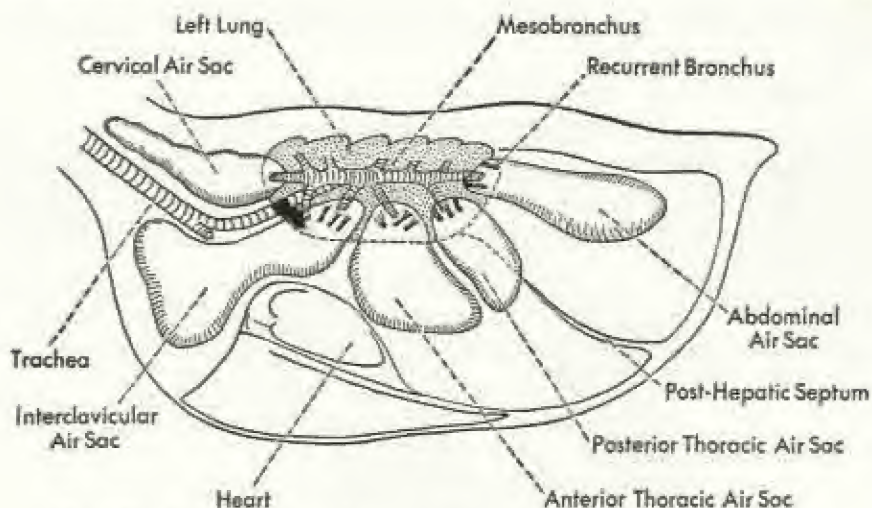


Fig. 342. Diagram of respiratory organs of a bird, left-side view. (After Goodrich.)

(Fig. 342). Surrounding the smallest bronchioles and opening into them are elaborate meshworks of minute air tubules surrounded by capillaries so that their walls serve as the actual respiratory surfaces (Fig. 343). It is possible, therefore, for the air to be drawn back and forth *entirely through* the air tubules of the lungs, with gaseous exchange taking place both on the way through the lungs to the air sacs as well as on the return. The air in the lungs of other animals is never entirely renewed with each respiration, as in

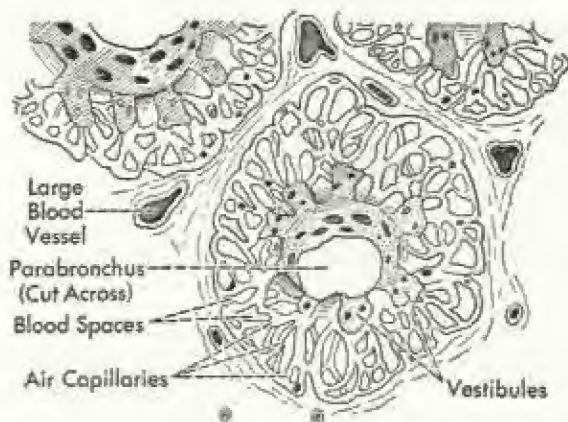


Fig. 343. Diagrammatic thick section of a small portion of a bird's lung, much enlarged. Vestibules are parabronchial outpocketings into which air-capillaries open. Spaces between air-capillaries have an abundant supply of blood capillaries. (After Goodrich.)

birds, since some of it regularly remains stagnated in the alveolar terminals.

Embryonically air sacs sprout out from the lungs at various points and extend into the body cavity, occupying spaces between the viscera; beneath the skin (in pelicans); between the muscles, supporting and connective tissues; between and around the joints of the cervical vertebrae; and penetrating even into the pneumatic cavities of the hollow bones (Fig. 344).

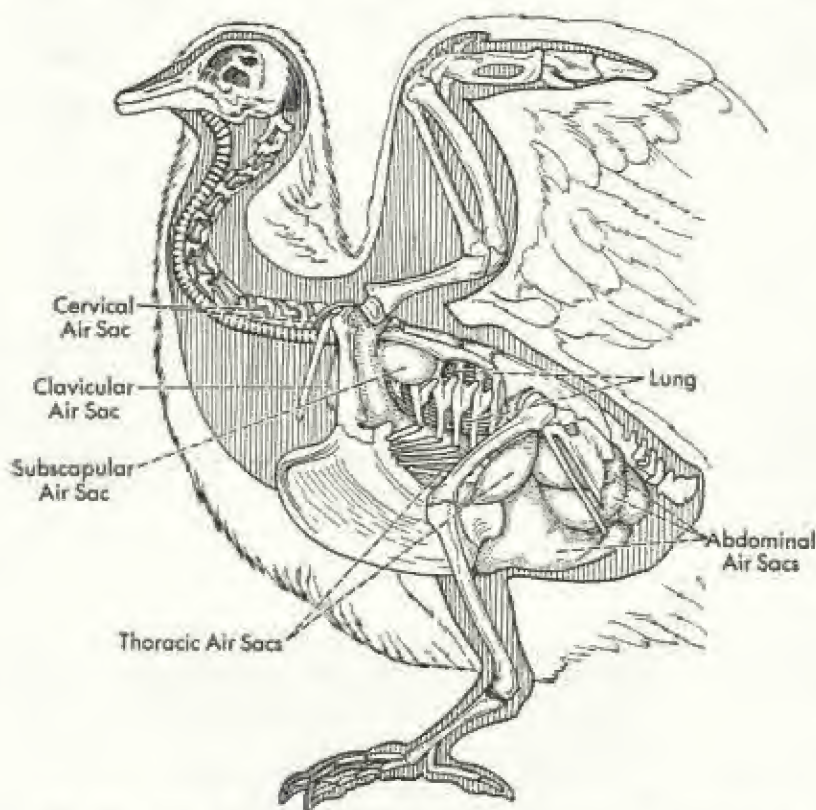


Fig. 344. The injected air sacs of a pigeon, showing how completely they occupy all available spaces. (After Müller.)

The primitive *Apteryx* of New Zealand alone has much reduced air sacs that do not enter the bones or penetrate the transverse septum to invade the body cavity.

Although the air sacs of the bird's lung are not supplied to any great extent with a capillary network, and consequently are not directly respiratory in function, yet they have several different uses, acting as bellows, bal-

loons, ballast, friction pads, heat regulators, reservoirs, and resonance aids to the voice.

On account of the inelasticity of the bird's lung, which is hampered by being anchored fast to the dorsal wall of the thoracic basket, some mechanical aid for effecting an efficient circulation of air through the lungs becomes all the more necessary. Such a mechanism is supplied by air sacs acting as *bellows*, enabling the air to be forced back and forth entirely through the lungs proper. In the capacity of *balloons*, the air sacs when inflated cause the specific gravity of the bird to be lessened owing to the intake and retention of heated air. Without this storage of warmed air it would require considerably more muscular effort to sustain a body heavier than air in suspension for considerable periods of time. Possibly inflated air sacs may also by their turgor aid mechanically in maintaining the wings in an extended position during soaring or volplaning.

As *ballast* the arrangement of the air sacs is such that a proper center of gravity may be established for balanced flight, and equilibrium easily maintained by shifting the air content of the sacs from one part of the body to another.

The insertion of air sacs like pads between the muscles *lessens friction*, thereby giving flexibility and grace to the aerial movements of birds. Because they are filled with warm moist air the air sacs help to *maintain and regulate the body temperature*, for the skin of birds in the absence of evaporating sweat is of little service for this purpose.

As *containers of reserve air*, the air sacs are undoubtedly useful. The muscular mechanism by which a resting bird causes air to enter the lungs, like that of mammals, involves the alternate elevation and depression of the breastbone through the activity of the intercostal muscles. It is necessary, however, during flight for the breastbone and the entire thoracic basket to remain firm, in order to insure substantial anchorage of the powerful flying muscles. To do this the intercostal respiratory muscles are held in tension and are for the time being not pumping fresh air into the lungs. Therefore, an internal reservoir of air is indispensable, while the flying muscles which ventilate the lungs by acting upon air sacs as bellows also control respiratory movements during flight. The more rapid the flight, the greater the automatic supply of air drawn through the lungs to and from the pneumatic chambers by the flight muscles. Violent action in mammals interferes with respiration, but with birds it enhances it. This is why fast flying birds do not "get out of breath," or probably suffer from "mountain sickness" in the air of high altitudes because the necessary increased wing strokes bring in a compensatory supply of rarefied air. The frigate bird, *Fregata*, that easily

maintains a rate of one hundred miles an hour, has about the best development of air sacs to be found in any bird.

The pneumatic diverticula of the lungs of *Chameleon*, already mentioned (Fig. 341), and those of certain other lizards may perhaps be regarded as prophetic of the air sacs of birds.

(e) **Mammals.**—The lungs of mammals are usually characterized in two ways: first, by being subdivided externally into two lobes; and secondly,

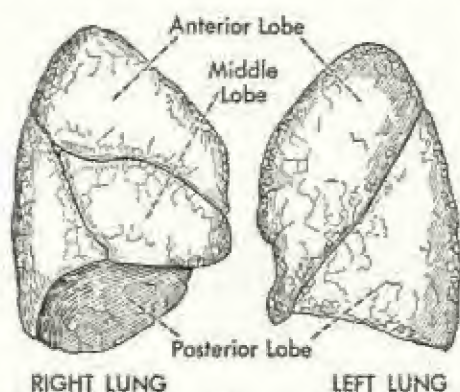


Fig. 345. Lobes of human lungs. Outlines of the outer, or costal, surface. (After Toldt.)

by showing some degree of asymmetry in accommodation to surrounding organs. When asymmetrical the lobes are more numerous on the right than on the left side. Thus, in man (Fig. 345), there are three lobes in the right lung and two in the left. The uppermost odd lobe of the right lung lies behind the right pulmonary artery, while the absence of a corresponding lobe on the left side permits the presence of the large left aortic arch.

Certain mammals, as for example Cetacea, Sirenia, Proboscidea, Hyracoidea, and most Perissodactyla, resemble other vertebrates in the absence of pulmonary lobes, while Monotremata are transitional, since they possess lobes only in the right lung.

The lungs of whales, which are located rather posteriorly in the hulls of these seagoing leviathans, are probably hydrostatic as well as respiratory in function. Whales have a unique breathing apparatus that enables them, during a plunge into the ocean depths, to imprison air in the capacious nasal chamber which is several times larger than the brain case. In fact the nasal chamber occupies the major part of a whale's head and is capable of storing a generous supply of air that would otherwise be forced out of the lungs by the enormous pressure of the water. The apertures leading from the nasal passages to the lungs can be shut off by two plugs of tissue which function like the stopper in a bathtub. As the air in the lungs becomes stale the plugs open long enough to exchange the stale air with pure air in the nasal reservoir, and when the whale finally comes to the surface the reservoir is emptied with considerable violence accompanied by confined water vapor, causing the excited whalers who witness the performance to shout, "Thar she blows!"

4. Pleural Envelopes

The lungs of higher vertebrates are enclosed in compartments called *pleural cavities*, separated from the abdominal cavity which is the storehouse of most of the internal organs.

The establishment in mammals of exclusive chambers for the lungs has been a gradual evolutionary process. The primitive lungs of amphibians push down into the general body cavity, carrying with them a thin covering of serosa continuous with the peritoneum that lines this common cavity but without the formation of independent pleural chambers.

In reptiles, along with the formation of a *transverse septum* formed by the invasion of peritoneal folds and the assurance of privacy for the heart by the partitioning off of a pericardial chamber, there is formed around the lungs a second envelope, also derived from the peritoneal serosa, that constitutes the outer, or *parietal*, wall of the pleural cavity (Fig. 336). The inner, or *visceral*, wall is the original derivative of the peritoneum already mentioned, and this intimately invests the lungs like a tight-fitting garment.

The space between the parietal and visceral walls, that is, the *pleural cavity*, is filled with a serous lubricating fluid which allows freedom of movement on the part of the extensible lungs within the pleural space.

5. Origin of the Lungs

The lungs, like the swim bladder, probably come from rudimentary gill pouches. While the swim bladder is usually a dorsal outgrowth from the floor of the foregut, the first evidence of lungs in man, which may be seen about the third week of fetal life, is a ventral groove on the floor of the same region from which the swim bladder sprouts out *dorsally*. As this groove

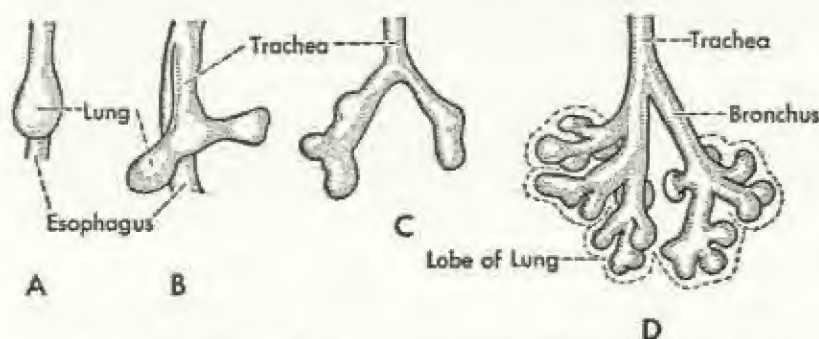


Fig. 346. Early stages in the development of lungs, trachea, and bronchi of human embryos. Ventral views. A, 4 mm embryo; B, 5 mm embryo; C, 7 mm embryo; D, 10 mm embryo. (After Arcy; A, after Grosser and Heiss; B, C, D, after Heiss and Merkel.)

pushes deeper down, it forms a single bud that soon becomes a bilobed sac representing the future lungs (Fig. 346). Soon after, a common stem or duct is formed by a further outgrowth of the lung sacs. This is the trachea, whose appearance is followed by the branching bronchi, and last of all by the elaboration of subdivisions within the lung sacs and the establishment of the alveoli.

During the differentiation of the lung sacs the endodermal lining invades the surrounding mesoderm, as shown by Moser in a series of illuminating diagrams (Fig. 347), with the end result that a maximum surface of respiratory endodermal tissue is brought into intimate contact, back to back, with vascular mesodermal tissue carrying blood-filled capillaries.

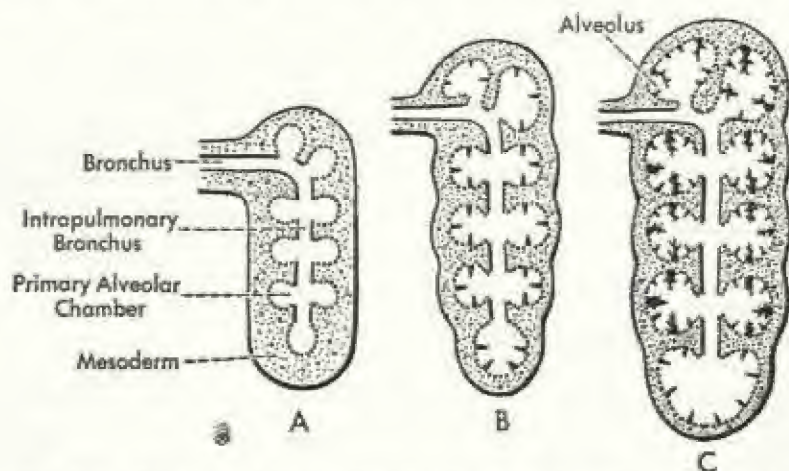


Fig. 347. Diagram of the formation of the lungs in turtles. A, intrapulmonary bronchus with several primary alveolar chambers invading the surrounding mesoderm; B, intermediate stage; C, the adult condition. The chambers have become subdivided into alveoli by ingrowth of their walls. Mesoderm reduced to partitions between the chambers. (After Moser.)

Human lungs assume definite shape before the end of the third month, although they do not take on their respiratory function as long as the embryonic placenta is active and are not entirely inflated for three or four days after birth. The alveoli are laid down by the seventh month and thereafter merely undergo enlargement.

V. DEVICES FOR SECURING AIR

The process of breathing demands more than a mechanism that simply allows blood and air to get together within osmotic distance of each other,

since there must also be present means for securing a continuous circulation of fresh air across the respiratory surfaces.

1. Fishes

In the case of submerged fishes, water charged with various gases, including the essential oxygen, enters either the mouth or the spiracles and passes out through the gill slits. It is forwarded and directed in its course, not only by muscular movements which alternately expand and contract the walls of the orobranchial chamber, but also by a system of valves that prevents the water from going the wrong way.

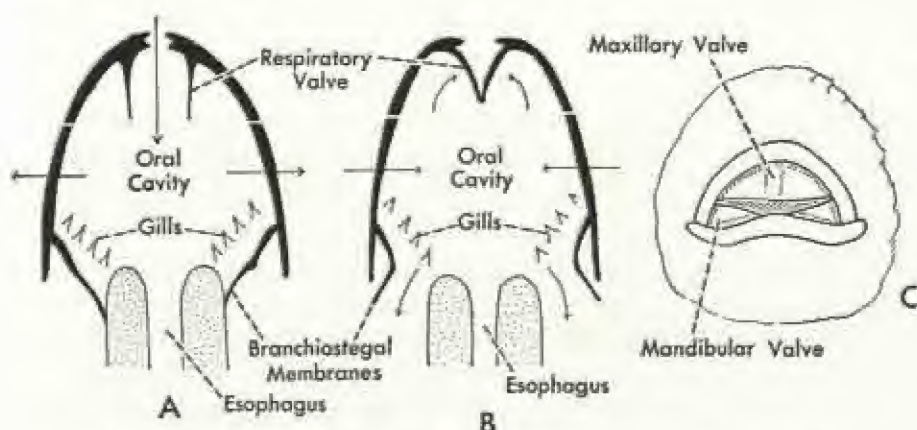


Fig. 348. Diagrams illustrating the mechanism of respiration in teleosts. A, phase of inspiration; B, phase of expiration; C, anterior view of the mouth valves. In A and B the anterior part (in front of break in wall of oral cavity) represents a vertical section, and the posterior part (in the vicinity of the gills) a horizontal section. Arrows indicate direction of water current and pressure, and those passing through walls of oral cavity the expansion and contraction of the opercular apparatus. In A, the respiratory valves (maxillary and mandibular) are open, and the branchiostegal membranes closed. In B, this condition is reversed. (A and B, after Dahlgren, from Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers; C, after Kingsley.)

The anterior set of these valves are collapsible folds along the inner edge of the mouth opening, those of the upper edge being called *maxillary*, and of the lower, *mandibular*. They reach their greatest differentiation in teleost fishes which have a well-developed opercular apparatus. The posterior, or *branchiostegal*, set of valves are membranes along the free margins of the opercular flaps (Fig. 348). A freely moving current of water is produced in

the following way. First, the mouth remains open as a narrow slit, while the anterior maxillary and mandibular valves lie flat, or open, and the posterior branchiostegal valves close. Next the walls of the orobranchial chamber spread apart by muscular action, thus pulling water into the mouth to occupy the increased space. Then the valves reverse, that is the anterior ones close the slitlike mouth aperture and the posterior ones open the opercular slit, while the walls of the orobranchial cavity squeeze together, forcing the water backward over the gills and out of the opercular openings.

In some teleosts, particularly those that feed on microscopic plankton, the branchiostegal valves play the major rôle in this process, but in others, for example the Percidae and the Sciaenidae, the opercular flaps take the most prominent part.

2. Amphibians

Amphibians never breathe through the open mouth but instead inspire air through the nostrils and the *choanae*, as the newly-established passageways into the mouth cavity are called. They are not even able to exercise emergency breathing through the mouth, as mammals do, for as long as the mouth remains open there is no way to compel the air to enter the lungs.

Necturus and other perennibranchiate urodeles sometimes come to the surface of the water and gulp air through the mouth, which may soon be seen escaping in the form of bubbles through the gill slits, although it is doubtful whether much of it reaches the lungs. This occasional air-gulping behavior does not furnish fresh air for the external gills that hang outside the gill slits, since by means of muscles that cause them to wave back and forth, these animals obtain their supply of oxygen dissolved in the water.

The intake of air in the frog, which may be taken as a representative of the anurans, is accomplished by a combination of pumplike throat muscles and nostril valves (Fig. 349). It will be seen that when the nostril valves open in the manner of lids and the throat muscles draw down, the oral cavity within is enlarged and air is necessarily inhaled. With the closure of the nostril valves and the contraction of the throat muscles, the lungs automatically become filled by the mouthful of air that is forced backward. The expiration of air alternates with inhalation and is accomplished by means of the contraction of body muscles.

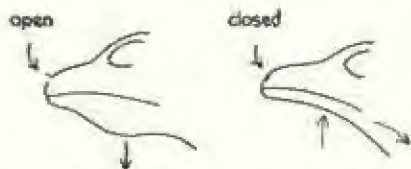


Fig. 349. Breathing mechanism of a frog.

3. Reptiles

The problem of getting air into the lungs of reptiles is much like that in the case of amphibians, although some improvement is seen since ribs and rib muscles furnish a mechanical means for admitting air that is not present in the practically ribless amphibians. This improvement, however, is ineffective in turtles, whose ribs form a boxlike armor of uncompromising rigidity. These animals still resort to the amphibian method of utilizing throat muscles and nostril valves, swallowing the air by "working the throat." No doubt the in-and-out movements of the turtle's head and neck aid in pumping air into the lungs while the pectoral muscles, which are *inside of the ribs* in these bizarre reptiles instead of outside as in other vertebrates, are aided by the abdominal muscles in bringing about the expulsion of air from the lungs. The usefulness of rib muscles in pumping air in and out of the lungs is very apparent in the panting snakes, lizards, and alligators.

The latter have an exceptionally elongated nasal passage-way with a curtain, or *velum*, that closes off the inner choanal openings from the mouth cavity. This device makes it possible for the alligator to breathe with the mouth open under water while holding the drowning prey between the cavernous jaws, only the tip of the snout with the openings of the external nares being above the water line (Fig. 350).

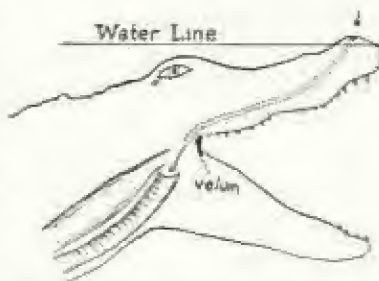


Fig. 350. Diagram to show respiratory passage (dotted) in an alligator. It leads to the trachea behind a flaplike *velum* in the back part of the mouth cavity, which enables the animal to breathe under water and at the same time to drown its prey held between the jaws, so long as the external nostrils are above the water line.

4. Birds

So long as a bird is not in flight it breathes by means of its rib muscles after the typical reptilian manner. When a bird flies, however, as already explained, the powerful pectoral muscles, on which flight depends, require and secure anchorage upon a rigid thoracic basket that does not change shape with every breath. The bellows-like air sacs, which are filled and emptied by the action of the flying muscles rather than the rib muscles, furnish an effective means for irrigating the lungs of a flying bird with air, while the inactive rib muscles remain temporarily fixed and rigid.

5. Mammals

In mammals both nasal and oral breathing are made possible by the backward migration of the glottis to a position in the posterior region in the throat. Nasal breathing, however, with the greater facilities thus provided for warming and moistening the inhaled air, and the added advantage of testing its quality by means of its passage over the sensitive olfactory surfaces in the nasal chamber, is the better and more favored method among mammals generally.

The outstanding advance in the breathing mechanism of mammals is furnished by the *muscular diaphragm*, which in lower vertebrates is foreshadowed by the transverse septum that separates pleural and pericardial chambers from the body cavity. The diaphragm consists of a central tendinous component, from which extend radiating muscle fibers derived from mid-cervical myotomes. The diaphragm when relaxed is shaped somewhat like an arched vault (Figs. 336 and 351), and is perforated by the dorsal aorta, esophagus, azygos vein, thoracic duct, postcava, and vagus nerve. As its radiating fibers shorten by contraction, the vault of the cuplike diaphragm lowers or flattens, thus increasing the space within the thoracic cavity. Consequently the atmospheric pressure from without forces air into the lungs. At the same time the viscera within the body cavity are crowded down so that the abdominal wall bulges out. The muscular opponents of the diaphragm are the strong walls of the abdomen.

In addition to abdominal diaphragmic breathing, mammals also utilize the reptilian method of rib muscles to enlarge the thoracic cavity when inspiring air. The ribs are bent, like jointed levers at an oblique angle to the vertebral column, and if acted upon by the intercostal muscles the movable sternum, to which they are attached ventrally, moves farther away from the relatively stationary backbone, thus enlarging the thoracic cavity in which the lungs are located. So it comes about that inspiration is effected not only by the depression of the diaphragm but also by the elevation of the ribs, both efforts calling for muscular activity.

Expiration, on the other hand, is to a large extent automatic through the elasticity of the stretched body walls, the taut cartilaginous ends of the bent ribs, and the tensility of the expanded lung tissues.

In big heavy animals, abdominal or diaphragmic breathing predominates over rib breathing. Jumping animals, like kangaroos and monkeys, utilize rib muscles rather more than the diaphragm in respiration.

Breathing by means of the ribs is also more pronounced in human females than in males in whom abdominal breathing predominates. The

reason for the sexual difference in the respiratory mechanism may be an evolutionary adaptation brought about in connection with pregnancy, during which period the presence of a growing fetus interferes somewhat with freedom of movement of the diaphragm.

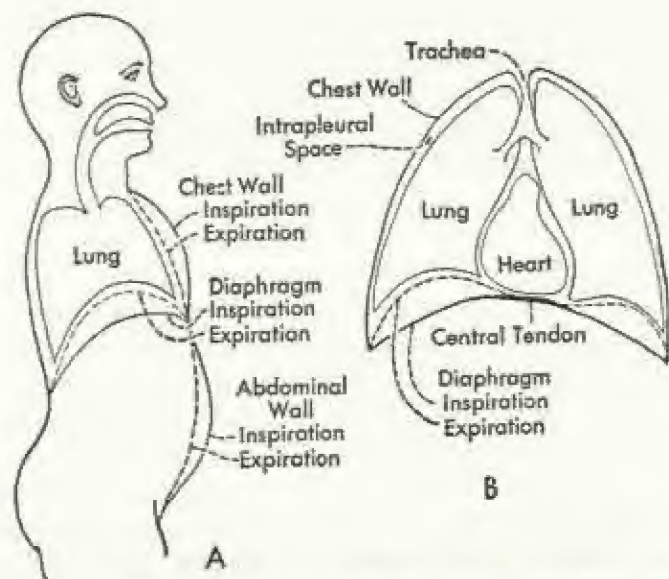


Fig. 351. Abdominal and thoracic contours during respiration. **A**, the relative positions of the chest wall, the diaphragm, and the abdominal wall at the end of maximal inspiration and expiration; **B**, diaphragm at end of normal inspiration and expiration. In quiet breathing there is no marked change in the position of the central tendon; in forced inspiration it may be drawn posteriorly, pulling the heart down with it. (From Howell, Fulton, *Human Physiology*, copyright 1946, by permission of W. B. Saunders Company, publishers.)

The amount of air required daily by a human being varies within wide limits but may average over 10,000 liters, including over 2000 liters of oxygen. The lungs of an adult may have an average capacity of 4000 cc of which some 500 cc, called *tidal air*, is renewed with every breath. Of the remainder, about 2500 cc is *complemental air* that can be inspired on occasion by deep breathing at the end of a normal inspiration of tidal air. The other 1000 cc is *supplemental air*, or the amount which can theoretically be forcibly expired after a normal expiration. After the deepest possible expiration there is still about a liter of air left in the lungs and respiratory tract. This *residual air* is not included in the data for lung capacity, as given above.

VL. VOICE APPARATUS

The emotions of animals are frequently expressed in various ways by characteristic movements and noises. Male rabbits sound an alarm by pounding the ground with their hind feet, while bucks and bulls send forth a resounding challenge by stamping with their front hoofs. Rattlesnakes shake their caudal castanets and many stridulating insects express themselves audibly by rubbing hard parts together.

Among vertebrates that produce a distinctive noise, the voice apparatus is generally a wind instrument, and consequently a direct part of the respiratory system.

The majority of vertebrates are dumb. Fishes, which outnumber all other vertebrates in species as well as individuals, have only a few representatives, such as drumfishes and "grunters," that break the piscine vow of silence.

Amphibians, excluding the musical frogs and toads, are practically voiceless, and reptiles also, if a few unusual cases such as hissing snakes, guttural geckos, and bellowing bull alligators are omitted, are prevailingly silent.

When King Solomon ecstatically sang in a springtime of long ago, "The flowers appear on the earth; the time of the singing of birds is come and the voice of the turtle is heard in our land," he did not refer to the silent reptile of that name, which is quite unable to celebrate the changing seasons vocally, but to the plaintive notes of the turtle dove.

Some moralist has pointed out the fact that probably the first vocal words spoken on this earth were the words of the croaking frogs, which sound like "*work, work, work.*" It should be noted in passing that the sedentary frogs, like many other armchair givers of advice, pay no heed to their own exhortations.

Birds as a rule are notably vociferous but there are numerous species, such as the stately storks, that preserve a dignified silence, while it is a curious fact that among mammals gigantic whales have relatively less voice than tiny squeaking mice.

The words in common use to describe sounds produced by mammals indicate a wide variety of distinctive "voices," with corresponding diversity in the wind instruments involved. For example, the horse "whinnies"; the cow "moos"; the donkey "brays"; the pig "squeals"; the sheep "bleats"; the elephant "trumpets"; the porcupine "grunts"; the lion "roars"; the cat "purrs"; the wolf "howls"; the dog "barks"; the rat "squeaks"; the lemur "wails"; the monkey "chatters"; and some human beings "sing."

Since most voices are dependent upon the expulsion of air from the lungs, the vocal apparatus, or *larynx*, is advantageously located around the

glottis, that is, the slitlike entrance to the trachea. Different sounds are produced by modifying the shape of the aperture and the contour of the cavity through which expelled air escapes. The cartilages, membranes, walls, and muscles of the larynx constitute a mechanism for effecting this result.

The mouth cavity in man, as well as the pliable cheeks and flexible tongue, aid greatly in altering the character of the chamber through which the column of air from the lungs is forced, thus changing the sounds produced. This can be easily demonstrated by pronouncing the vowels, *A, E, I, O, U*, in succession and mentally noting the changes that meanwhile result in the position of the lips, tongue, and cheeks, and the consequent alteration in the contour of the mouth cavity while executing these distinctive sounds.

In this connection it is a suggestive fact that the evolution of voice has a close dependence upon emergence from water to life in air. It is obvious that the traditional episode of the Tower of Babel could only have been staged very late in the evolutionary story, after the human larynx had come into its own.

1. Amphibians

There is no true larynx in fishes, but in voiceless salamanders the larynx consists of two tiny triangular guardian cartilages, *lateral cartilages* (Fig. 352), embedded one on either side of the glottis. In some cases when there is enough trachea to permit, as for example in *Siren*, there are additional fragmentary cartilaginous rings below the laterals. These prophetic carti-

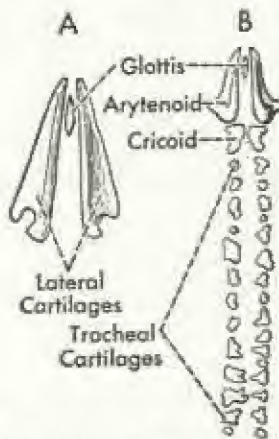


Fig. 352. Laryngeal cartilages of urodeles. A, *Necroturus*; B, *Siren*. (After Wiedersheim.)

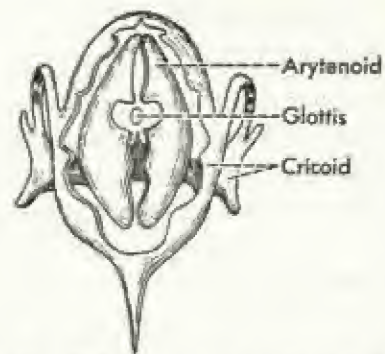


Fig. 353. Laryngeal apparatus of a frog. (After Wiedersheim.)

lages of urodeles become developed into elongated laryngeal cartilages in the musical frogs, toads, and hylas. The "brek-ek-ek-kex, ko-ax, ko-ax" of Aristophanes' famous frogs, imitated in one of the modern college yells, is a characteristic bit of virile vocalization familiar to everyone whose experiences include a frog pond in springtime. The mechanism by which these haunting nocturnes are produced consists of a pair of *arytenoid cartilages*, and in addition, of a new cartilage, the *cricoid*, which is an elaboration of the first tracheal ring or rings (Fig. 353). Dilator and adductor muscles operate these skeletal elements.



Fig. 354. *Hyla*, showing inflated resonance sac. (After Boulenger.)

Two folds on the inner walls of the laryngotracheal chamber, the *vocal cords*, lie parallel with the slitlike glottis. The Anura, especially the males of the species, have besides, internal *vocal sacs* in the throat region which are apparent externally when inflated. These serve as chambers of resonance for increasing the carrying quality of their vocalizations. A single median vocal sac is common to all hylas (Fig. 354), as well as the toad, *Bufo*, while two lateral sacs show at the shoulders of frogs, being especially pronounced in the male bullfrog, *Rana catesbiana*, when its twanging "jug-o'-rum" note is being broadcast.

As a matter of fact the lungs of frogs and toads are largely organs for producing sound after the manner of bagpipes, the respiratory function being taken care of mostly by the skin, as shown by the fact that the cutaneous arteries exceed the pulmonary arteries in size.

2. Reptiles and Birds

Reptiles and birds have less larynx and more trachea than Anura. Compensating this deficiency, birds have evolved an additional secondary "larynx," called the *syrix*, which is located at the lower end of the trachea at its junction with the bronchi, instead of near the glottis (Fig. 355). The position of this unique voicebox is in line with the extreme structural modifications of birds whereby all possible weight is centralized for purposes of equilibrium in flight.

There are no vocal cords in the reduced larynx of birds. Instead sounds are due to vibrations of membranes in the syrix. The median wall of the

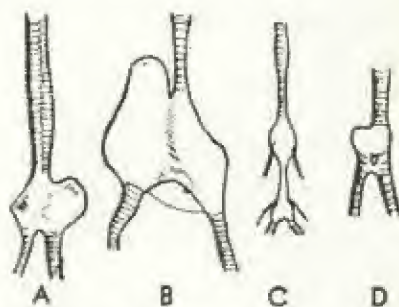


Fig. 355. Different syringes. A, mallard; B, goosander; C, velvet scoter; D, eider duck. (After Pyecraft.)

beginning of each bronchus is a thin *membrana tympaniformis interna* (Fig. 356). As there is a projection of the interclavicular air sac which lies between the bases of the bronchi, the tympaniform membranes can vibrate as air is expelled past them. In singing birds there is also an unpaired vibratory *membrana semilunaris*, extending dorso-ventrally near the junction of the bronchi and trachea. A bony ridge, the *pessulus*, supports the semilunar membrane. The cartilages of the syrinx, which are modifications of tracheal and bronchial rings, are combined with intercartilages, membranous walls, and a variety of muscles, into an efficient vocal mechanism. By means of this apparatus the bird is enabled to change the shape of the tracheo-bronchial chamber, thus producing a variety of different sounds.

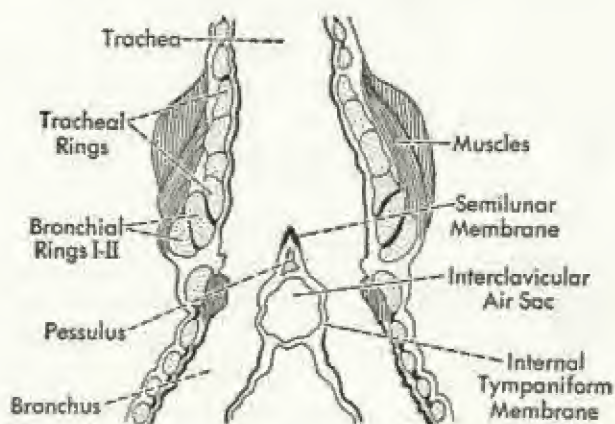


Fig. 356. Longitudinal section through the syrinx of a thrush. (After Haecker.)

3. Mammals

The cartilages of the mammalian larynx include, in addition to a pair of triangular *arytenoids* around the glottis, and a bandlike *cricoid* just below, a relatively large quadrilateral shieldshaped ventral *thyroid cartilage*, that in man forms the movable prominence in the neck known in academic circles as the *pomum Adami*, and elsewhere as "Adam's apple."

The thyroid cartilage is originally paired, as shown by the fact that in monotremes it is made up of two separate lateral plates instead of a single piece, and in all mammals it is derived embryonically from the remains of paired branchial arches.

Still another structure developed in mammals is a cartilaginous lid above the glottis, called the *epiglottis*. This aids in closing off the tracheal tube

from food that is passing down to the esophagus, a process accomplished not so much by the closing down of the epiglottis as by the elevation of the tracheal tube to fit against the overhanging lid. That the larynx is temporarily elevated during the act of swallowing is easily demonstrated by placing the thumb and finger lightly against the Adam's apple, at the same time imitating the transit of food by swallowing.

Furthermore, in mammals the horseshoe-shaped *hyoid bone*, situated above the glottis region, is made a part of the laryngeal complex by connecting ligaments which suspend the larynx. In addition certain minor laryngeal cartilages are described in human anatomy, for example, two minute rod-like *cuneiform cartilages of Wrisberg*, in the fold between the epiglottis and the arytenoids; two small conical nodules, the *cartilages of Santorini*, surmounting the apices of the arytenoids; and the *triticeous cartilages*, embedded in the ligaments connecting the hyoid bone on either side with the thyroid cartilage, so called because of a resemblance to grains of wheat (*Triticum*). The location and relationships of the most important cartilages that make up the laryngeal voicebox of man are indicated in Figure 357.

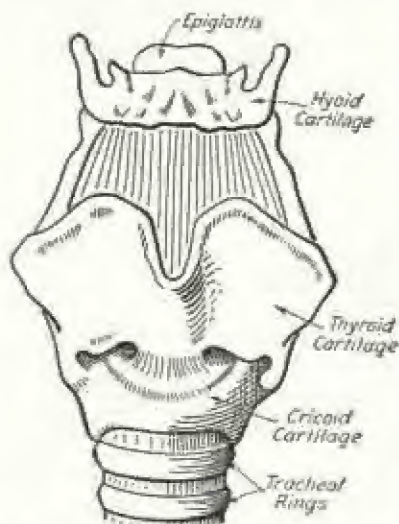


Fig. 357. Front view of human larynx. (After Cunningham.)

The vocal cords, which reach their greatest differentiation in mammals, are two pairs of handlike folds on the inner wall of the larynx, one above the other, extending between the arytenoids and the thyroid cartilage (Fig. 358). Of these the upper pair are called "false," and the lower pair "true" vocal cords. Made up of dense bands of elastic fibers covered over by mucous membrane, their position and tension may be altered by means of accompanying muscles. During ordinary breathing they do not vibrate sufficiently to produce sound, but when desired the column of air that is forced over their surface is modified through their activity into audible vibrations.

In most cases sound is produced by *expiration* of air over the vocal cords, although in exceptional instances, a familiar example of which is the "hee-haw" of the donkey, the air does vocal service both going in and coming out.

Between the true and false vocal cords a groove or concavity, known as

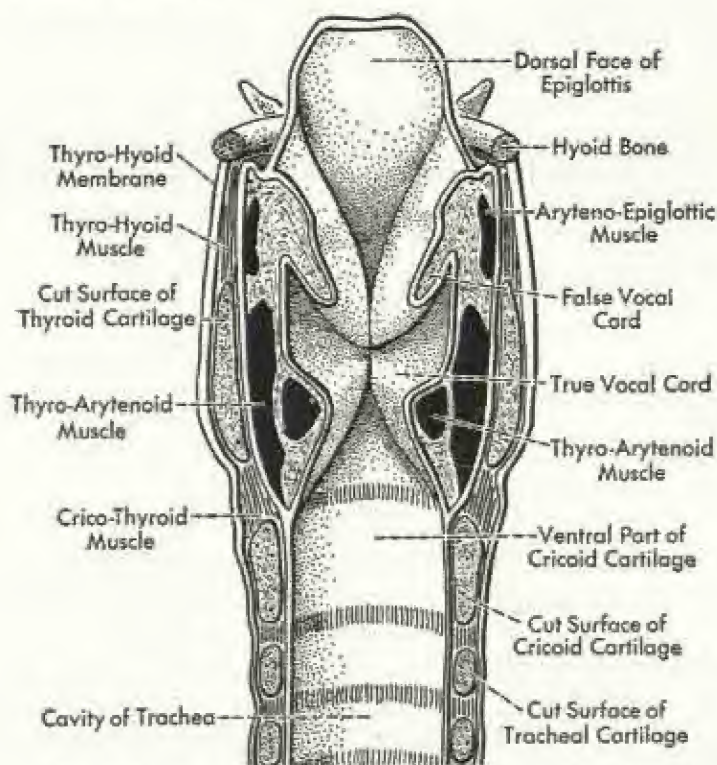


Fig. 358. Vertical section of human larynx. (After Testut.)

the *ventriculus laryngis Morgagni*, which is particularly well-developed in certain howling monkeys and vociferous apes, has the capacity of swelling out on either side into air-filled resonance sacs that function much as do similar structures in frogs, by adding intensity to the sounds produced. Curiously elephants are without false vocal cords, while hippopotami have no others.

In young marsupials that remain attached to the nipples of the mother for protracted periods by means of an automatic sphincter muscle around the mouth, the larynx becomes so elongated that it extends up into the nasopharynx behind the soft palate, enabling these young animals to breathe and take in milk at the same time.

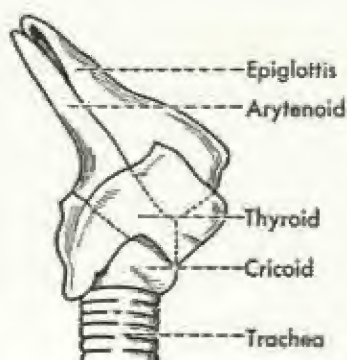


Fig. 359. Larynx of *Ziphius*, a whale. Anterior ends of elongate epiglottis and arytenoids extend forward into nasopharynx. (After Gegenbaur.)

This device eliminates complications usually attendant upon the double traffic of air and food in the pharyngeal crossing of the ways.

Whales have an elongated larynx which extends into the nasopharynx so far that the glottis can be enwrapped by the soft palate, an arrangement that mitigates some of the difficulties to which these aberrant mammals are subjected by their marine existence (Fig. 359).

Outgo Apparatus—Excretory System

I. EXCRETION

The inevitable consequence of the metabolic processes characterizing living creatures is that various by-products are formed in the body that must be got rid of for the reason that they not only are useless to the organism but may become decidedly harmful if retained.

Since there are many kinds of animals, there is a variety of devices for accomplishing this universal function. Excretions should not be confused with glandular secretions, such as saliva, milk, tears, mucus, enzymes, and hormones, which are of service to the organism. The mechanism of sewage disposal is the *excretory apparatus*.

The substances eliminated by excretion may be in the form of gases, solids, or liquids. Lungs and gills furnish the principal mechanism for the excretion of the gas *carbon dioxide*, resulting from the respiratory oxidation of carbohydrate and fat foods, while the digestive tube is the avenue of escape for the solid refuse from ingested food. Although the latter may not be regarded as true excretion, since the solids evacuated have never been incorporated as a part of the body, it is nevertheless an indispensable part in the process of the disposal of waste. Both of these methods of elimination have already been considered in the foregoing chapters upon the digestive and respiratory apparatus.

In addition to these two methods of disposal of the unusable products of the body, there is also a constant excretion, or sloughing off, of cellular material from the epithelial surfaces of the body, both from the outer exposed surface, and also from the lining of various tubes and ducts which have access directly or indirectly to the outside.

The present chapter is concerned primarily with the disposal of *liquid waste* by means of the urinary apparatus which is ordinarily referred to as the "excretory system."

As a matter of fact liquid, or water in various guises, is disposed of in the animal organism through several different channels. It is thrown off

from the lungs and the sweating skin of mammals as vapor; from the digestive tract as the fluid component of the feces; and above all from the kidneys in the form of *urine*. It comes to the kidneys from the blood, charged with salts in solution, both organic and inorganic, together with a variety of other chemical substances, as well as cell wreckage of various sorts.

Probably the simplest urinary apparatus of excretion is the *contractile vacuole* in protozoans, which periodically expels its liquid contents, accumulated from the surrounding substance of the cell to the outside.

In the bloodless flatworms (planarians) excretion is accomplished through a system of branching ducts that ramify throughout the body and join before emptying their excretory contents to the outside. The numerous extreme tips of this hollow branching system end blindly in swollen knobs, called *flame cells*, because in the cavity within them there is a tuft of cilia whose flamelike flickering motion forwards the collected waste liquid on its outward way from the surrounding tissues.

In animals having a body cavity, drainage tubes, or *nephridia*, are introduced connecting the cavity with the outside. When nephridia occur in invertebrates they are typically paired and independent of each other, but in vertebrates they are more or less massed together into definite organs of excretion, known as *kidneys*. Primarily nephridia open at one end into the body cavity and at the other, either independently or indirectly, through a common connecting duct to the outside. This furnishes a means of escape for the coelomic fluid in the body cavity, which receives contributions by way of the blood from all parts of the body. Such an arrangement is of particular significance in many invertebrates, for example annelid worms, although decreasing in importance among vertebrates. On account of the lessening usefulness of the coelomic fluid in the absence of an open blood system and the elaboration of a closed blood system, the liquid wastes of vertebrates are collected directly by the blood stream rather than after finding temporary sanctuary in the coelom.

The excretory system of vertebrates may be described, therefore, as fundamentally made up of nephridia, more or less completely emancipated from the original direct connection with the body cavity, but nevertheless in intimate osmotic contact with blood capillaries by means of which waste materials are collected from the blood stream and transferred to the outside through ducts of exit.

The nephridial tubes of the kidneys have structurally much in common with the sweat glands of the mammalian skin that have been described as minute supplementary kidneys. Both are tubes with walls of excreting cells in close juxtaposition to capillaries, and have the power of abstracting waste

materials from the blood stream. When it is remembered that there are over 2,000,000 sweat glands in the skin of an ordinary human being, and that end to end they constitute over twenty-five miles of glandular tubing, according to Macfie, it will be realized that these microscopic structures are by no means insignificant understudies to the kidneys in the disposal of liquid waste materials from the body.

For purposes of general description the urinary apparatus of a typical vertebrate may be considered under three headings: (1) kidneys; (2) urinary ducts; and (3) bladders.

II. KIDNEYS

I. Forms

With respect to the shape of the paired kidneys the evolutionary tendency is towards compactness and consequently there is a certain parallel between their form and the general contour of the body. The kidneys of the primitive eel-like cyclostomes are long straplike bands, while in fishes generally they extend not only throughout the length of the body cavity but also they may penetrate even beyond into the tail musculature. Frequently too, the typical shape of the kidneys of fishes is modified to conform to the presence of the swim bladder, which in fishes is a bedfellow of these organs.

Among amphibians the wormlike *Gymnophiona* and the long-bodied urodeles have correspondingly elongated kidneys, narrower anteriorly and widening posteriorly, while in the squat anurans these organs become much more compact and rounded in shape.

Although lizards and alligators somewhat resemble urodeles superficially, the relation between the shape of the kidneys and the form of the body is less marked. The kidneys, however, are still somewhat elongated, but in turtles become decidedly compact, conforming to the rigid requirements of space imposed by the shell. The opposite extreme is shown by snakes that have the kidneys not only attenuated like the body but also entirely crowded out of the typical side by side position, so that they lie tandem-fashion one behind the other.

The concavities of the elaborate pelvis of birds, in which the kidneys are for the most part packed, form a restricting bony casket that determines their lobulated form. The highest degree of compactness is found among mammals.



Fig. 360. Left lobulated kidney of a bear, partly dissected. [After Hente.]

The bear (Fig. 360), ox, seal, walrus, and porpoise have *lobed kidneys*, a condition appearing also in human embryos but which becomes obliterated soon after birth.

Fusion of the two kidneys occurs frequently in fishes (Fig. 396), and in some lizards, at least at the posterior end, as well as in many birds. Posterior fusion of the kidneys may exceptionally appear even in man, when a so-called "horseshoe kidney" results.

If for any reason one of two kidneys is put out of commission, the other usually enlarges into a "compensating kidney," taking over the work of its incapacitated mate in addition to its own.

2. Position

The kidneys are closely associated with the dorsal wall of the body cavity where they lie outside of the peritoneum.

In fishes and birds they fit with intimate snugness along either side of the backbone, but in amphibians, reptiles, and mammals are less closely attached to the body wall, sometimes projecting into the body cavity (Fig. 361). In all of these classes the kidneys are usually *retroperitoneal*, behind the peritoneum, although in some mammals they may even hang free, enclosed in a peritoneal envelope which entirely surrounds them.

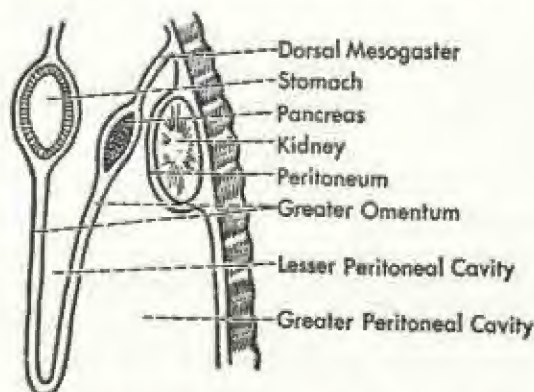


Fig. 361. Diagram showing position of kidney behind the peritoneum. (After Huntington.)

Symmetry of position is quite fixed in birds whose kidneys are rigidly held side by side in depressions of the pelvis, but it is less apparent in mammals where, being less restricted, one kidney is usually not exactly opposite the other. The left kidney in man is ordinarily situated at a somewhat higher level than the right, although many exceptions to this arrangement have been observed.

Each human kidney weighs about four and one-half ounces, and in its three major dimensions measures slightly more than four by two by one inches. It is shaped like a "kidney bean," with a convex lateral and a concave medial margin. The depression of the concave margin is the *hilus*, where the *renal artery* and the *nerves* enter and the *renal vein* and *ureter* make their exit (Fig. 362).

3. Gross Structure of the Mammalian Kidney

When split lengthwise in the frontal plane the mammalian kidney is seen to be a hollow organ with walls of very unequal thickness on the convex and the concave sides. The excentric cavity within is known as the *renal pelvis*. This cavity is really a funnel-shaped expansion of the urinary duct, or *ureter*. The thicker walls are the solid substance of the kidney itself, made up of a mass of nephridia, blood vessels, and connective tissue, which even to the naked eye appears to be differentiated into a narrow, outer, rather uniform *cortical zone*, and a wider, inner, more diversified *medullary zone*, bordering immediately on the renal pelvis. The entire structure is surrounded by a tightly fitting capsule of connective tissue, the *tunica fibrosa*.

The medullary zone presents a number of cone-shaped segments, the *Malpighian pyramids*, the bases of which rest against the cortical layer while the apices, *papillae*, project into the cavity of the pelvis. There are seven to twenty pyramids in the human kidney. Each cup-shaped part of the pelvis that surrounds a papilla is called a *calyx*. Between the Malpighian pyramids are masses of blood vessels, forming the *columns of Bertini*, that are made up of subdivisions of the renal arteries and veins on their way to and from the renal tubules of excretion which are crowded together in the Malpighian pyramids. The narrow outer layer of cortex, upon which the bases of the Malpighian pyramids rest, lies just underneath the tunica fibrosa. Due to the presence of the cortical rays, it has a striated appearance.

The kidneys of many animals, for example, *Echidna*, marsupials, insectivores, rodents, carnivores, perissodactyls, and apes, that are *unipyramidal*

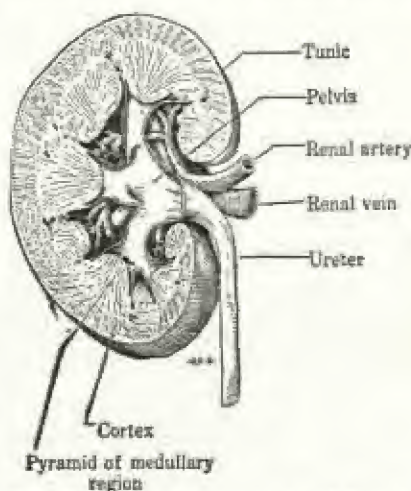


Fig. 362. Frontal section of human kidney. (From Woodruff, *Animal Biology*, copyright 1941, by permission of The Macmillan Company, publishers.)

with only a single papilla (Fig. 363), are never lobed, since the number of pyramids determines the number of lobes. The true multilobed condition of the human kidneys, which is most plainly apparent at about the fourth fetal month, is masked by the growth of parts which eventually fill in the interstices between the lobes. The relation of all these parts is described in the following section dealing with the microscopic structure of a single *urinary unit* or nephridial apparatus, and its position in the Malpighian pyramid.



Fig. 363. Evolution of pyramids in different kidneys. At the left is the unipyramidal type; in the center a lobulate kidney with several pyramids; and at the right, a kidney composed of several pyramids but tissue filled in between them so that it is no longer externally lobulate. (After Nuhn.)

4. A Urinary Unit

A urinary unit is a transformed nephridium that has gained an intimate connection with the blood system and established an avenue of drainage to the outside. The various parts of such a unit are pictured in Figure 364.

The junction where the nephridial tube makes contact with the blood stream is called the *renal corpuscle* (Fig. 365). It consists of a spherical tuft or knot of arterial capillaries, the *glomerulus*, enveloped by a double cup of epithelial cells, *Bowman's capsule*, between the double layers of which is the cavity of the renal tubule, or nephridium.

The formation of Bowman's capsule around the glomerulus at the tip of the renal tubule is brought about when the glomerulus comes into contact with the tip of the tubule and pushes it in from the outside, like the finger tip of an empty glove. The delicate inner cup of Bowman's capsule is thus closely adherent to the glomerulus so that the blood in the glomerular capillaries is separated from the cavity at the end of the renal tubule only by two exceedingly thin cell layers, that is the wall of the inner cup of Bowman's capsule and the wall of the glomerular capillary itself. Thus filtration of the liquids to be excreted from the blood into the nephridial tube is made easily possible. Once through the inner wall of Bowman's capsule, the excretory filtrate passes down the *neck* into a thick-walled, kinked-up glandular por-

tion of the tube, known as the *proximal convoluted tubule*, whence it continues around a non-glandular hairpin curve, *Henle's loop*, into a second thick-walled, kinked-up glandular part, the *distal convoluted tubule*, which opens in turn into a *collecting tubule* (Fig. 364). Eventually the collecting

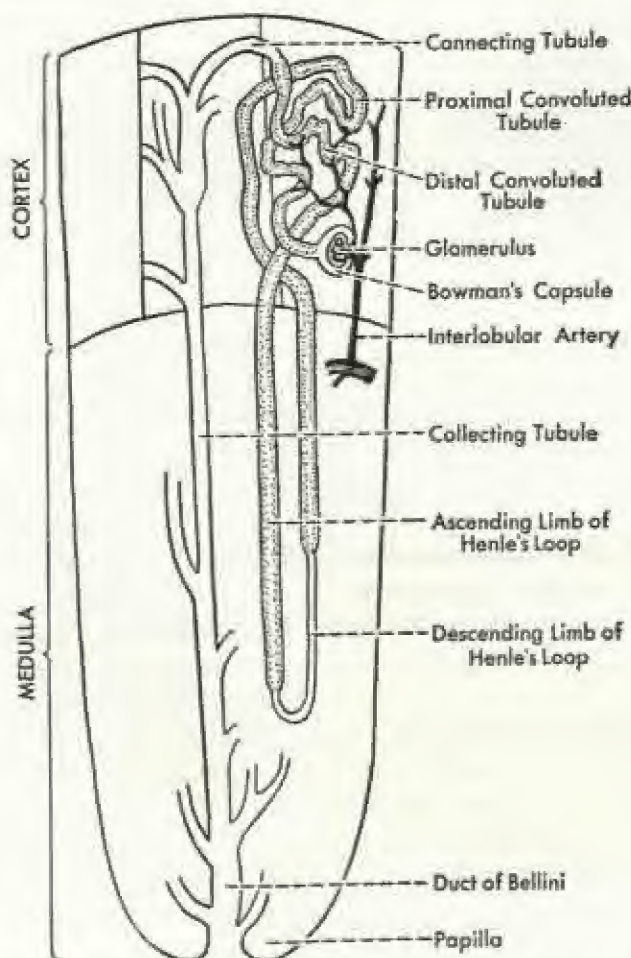


Fig. 364. Diagram of a urinary unit. (After Pietsol.)

tubules of neighboring units join into larger common channels, called the *ducts of Bellini*, that finally open into the renal pelvis at the tips of the papillae. Thus the entire urinary unit from glomerulus to pelvis is a continuous canal, the walls of which vary much in character and function. As many as ten to twenty-four ducts of Bellini, or *papillary ducts*, may empty into the calyx of the pelvis from a single papilla of the human kidney. It is

the pelvis, or enlarged end of the *ureter*, which, by way of the *bladder* and *urethra*, establishes a highway of communication with the outside world.

The blood stream passes through the kidney in the following manner (Fig. 366). The renal artery, entering at the hilus, subdivides in the columns of Bertini, then breaks up into

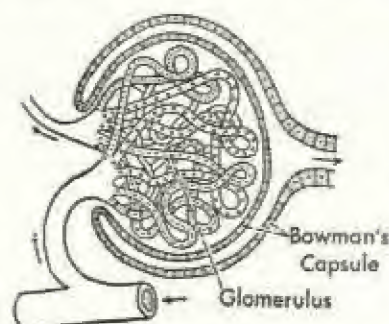


Fig. 365. Arrangement of capillaries in a glomerulus. Each branch of afferent arteriole continues, without anastomoses with the others, until all join to form efferent vessel. Afferent arteriole is larger than efferent one. (After Vimtrup.)

arterioles and finally capillaries in the cortex. The latter knot up into the glomeruli, which are entirely arterial, forming a *rete mirabile*, rather than an arterio-venous capillary transition. The afferent twig entering the glomerulus is larger than the efferent twig which makes its exit near by, on the same side that the afferent twig enters. The inequality in the size of these twigs tends to build a pressure within the glomerulus that is probably higher than in any other capillaries. The emerging efferent twig soon breaks up into a capillary network which entangles the convoluted tubules. Here in this capillary network the arterio-venous transition occurs, since at this point intimate

contact with the glandular walls of the convoluted tubules occurs, which makes possible the change in the blood from arterial to venous character.

The venules emerging from the capillary network anastomose with neighboring venules from other units in the cortex to form larger veins which run in the columns of Bertini between the Malpighian pyramids and finally join to form the renal vein that emerges from the kidney at the hilus.

The cortical region presents to the naked eye a granular appearance because in it are embedded the glomeruli and the convoluted tubules of the urinary units, while the striated appearance of the Malpighian pyramids is due to the presence of the parallel Henle's loops and the collecting tubules (Fig. 364).

It is estimated that the human kidneys may include as many as 2,000,000 urinary units that establish continuous open channels from the glomeruli to the pelvis, through which some of the components of the onward-rushing blood stream are diverted and eventually discarded.

The secretion of the urine probably involves two processes: (1) filtration at the glomerulus and (2) reabsorption at the convoluted tubules. Water and all other non-protein constituents of the blood plasma are filtered into the tubule at the glomerulus. This very dilute fluid is then concentrated

at the convoluted tubules by active secretion back into the blood stream of: 99 per cent of the water; all of such useful substances as glucose and amino acids; most of the inorganic ions such as sodium, chlorine, and potassium; little or none of the urea, uric acid, creatinin, and sulphate. It is possible that under certain conditions substances may be added to the urine in the tubules.

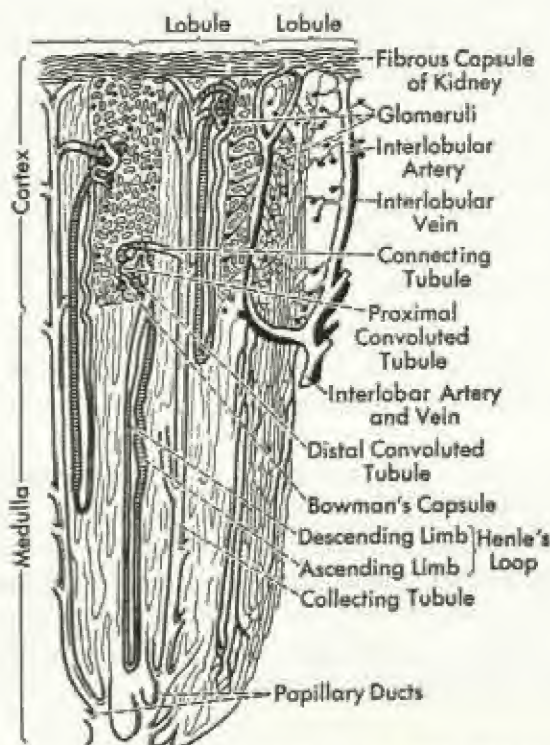


Fig. 366. Diagram showing the relation of urinary units to the circulatory system. (After Bailey.)

5. Urine

The composition of urine varies enormously in different animals and at different times in the same animal. This is because the blood from which the urinary excretion is obtained by the kidneys is such a kaleidoscopic modifiable fluid tissue that it reflects constantly different states of metabolism within the body. Furthermore, under pathological conditions still other variations from the normal in the composition of the urine appear. Consequently urine analysis is an important aid to the diagnostician in finding out what is going on within the body. This fact was realized even by the

medical practitioners of former centuries to whom the refined chemical technic of modern urine analysis was not available. At least certain abnormalities of urine could be discovered by simple visual inspection and this was very generally, and no doubt more or less oracularly, done. In the crude woodcuts of old medical books of the sixteenth and seventeenth centuries there recurs over and over again, like a motif in architecture or music, the *urine motif* in the form of a urine flask, which plainly tells the story of the importance given to the examination of samples of urine in the medical diagnosis of those days.

Carnivores generally have an acid urine, while that of herbivores tends to be alkaline, except when they are feeding largely upon milk. It is usually more concentrated in animals, such as turtles and birds, which drink sparingly. In man its specific gravity varies from 1.016 to 1.020, and normally about a liter and a half is produced every twenty-four hours.

Urine is characterized by nitrogenous waste products, such as urea, creatinin, hippuric acid, ammonia, and uric acid, although nitrogen-free constituents and inorganic substances, such as sodium chloride, and sulphates and phosphates of sodium, potassium, calcium, and magnesium are also present.

In mammals, amphibians, and fishes, urea, formed from the blood in the liver, is the prominent nitrogenous compound present, while in reptiles and birds, with a minimum of water as a component, it is uric acid.

Mitchell gives a table that accounts for about 99 per cent of the constituents in most human urines, in which 95.1 per cent is water; 2.55 per cent nitrogen-containing constituents; 1.26 per cent inorganic materials; and .052 per cent nitrogen-free substances.

III. URINARY DUCTS

The ducts that drain the paired kidneys are usually two, although some fishes may have six or eight supplementary ducts when the nephridial organs extend into the extensive tail region. In higher vertebrates the urinary ducts are termed *ureters*. These tubes with muscular walls and a comparatively small bore forward the continuous products of the kidneys, not by gravity alone, but by peristalsis regardless of the position of the body.

The length of the ureters depends upon the position of the kidneys within the body cavity. They are very long in snakes and extremely short in birds. In adult man they average from eleven to fourteen inches in length.

Urinary ducts terminate at the outside in various ways. In bony fishes, male amphibians, and monotremes, they unite with the sexual ducts into a

common channel, or *urogenital canal*, opening at the genital aperture. In elasmobranchs, most reptiles, and birds, they debouch into the cloaca, while in mammals they open into a reservoir, the *bladder*, whence by a second duct, the *urethra*, the outside is finally reached (Fig. 367).

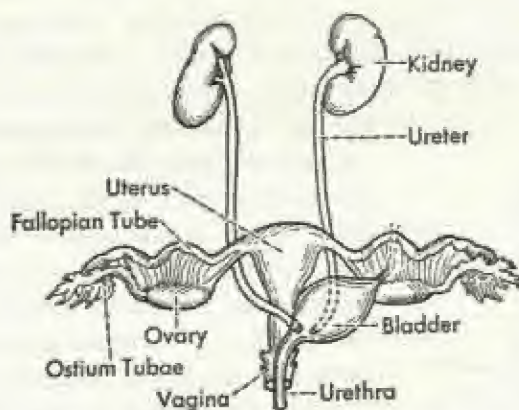


Fig. 367. Urogenital apparatus of female mammal.

IV. BLADDERS

The continuous excretion of liquids from the kidneys has given rise to the necessity for a temporary storage sac which may be emptied at suitable intervals. There are three general types of urinary sacs, or *bladders*, namely, tubal, cloacal, and allantoic.

Tubal bladders, which are present in most fishes from the ganoids on,

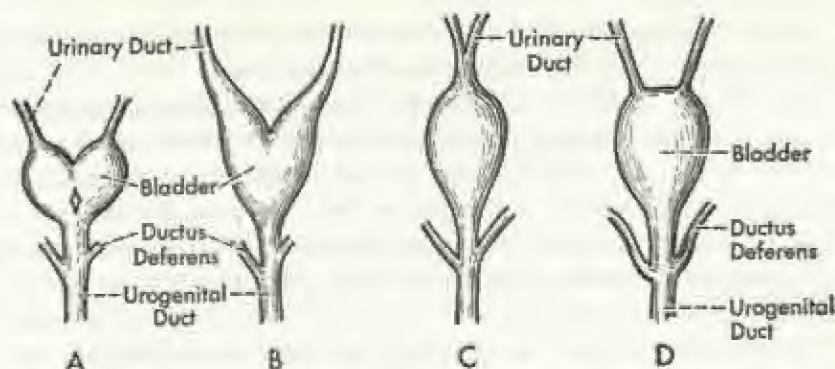


Fig. 368. Various types of urinary bladders in fishes. A, duplex type in *Gadus*; B, bicornis type in *Lepidosteus*; C and D, simplex type with united urinary ducts. (After Nuhn.)

are formed by the widening or enlargement of the urinary ducts. In many fishes two independent bladders may form, *vesica duplex* (Fig. 368A), one near the end of each urinary duct, with the two ducts afterwards uniting into a common passage-way of exit; or the two may run together into a common bilobed bladder *vesica bicornis* (Fig. 368B), as in *Lepidosteus* and some other ganoids; or finally, the two excretory ducts may first join and then expand into a single bladder, *vesica simplex* (Fig. 368C), as for example, in the pike, *Esox*. In all of these cases the urinary ducts enter at one

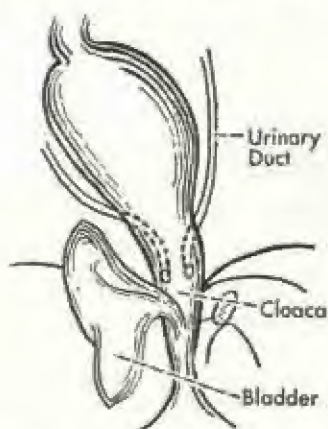


Fig. 369. Ventral view of cloacal bladder of an amphibian.

end of the bladder, while the exit is made at the opposite pole. The tubal bladder, which is frequently larger in the female than in the male, is most common in certain teleost fishes like the Pleuronectidae that have no swim bladder. It is somewhat difficult to account for the presence in fishes of these structures that are rarely absent yet of doubtful utility.

The *cloacal bladder* occurs in dipnoans, amphibians (Fig. 369), and monotremes. It is a diverticulum of the cloacal wall opposite the point where the urinary ducts, with which it has no direct connection, enter. It is located dorsally in lungfishes and ventrally in amphibians. In the perennibranchiate amphibians it is considerably elongated, but rounded and

broadened in frogs and toads. Frequently it is bilobed while in some urodeles, for example *Salamandra*, *Triton*, and *Eurycea*, the lobes are prolonged into hornlike processes.

Cloacal bladders are filled by the closure of the outer cloacal sphincter and the backing up of the urinary secretion into them.

The *allantoic bladder*, according to most embryologists, arises from the enlargement of the proximal or basal end of the embryonic allantoic stalk. It is characteristic of mammals and of such reptiles as turtles and certain lizards that have a bladder. In the case of other amniotes, like snakes, crocodiles, some lizards, and birds, the whole allantois degenerates without developing a bladder. In mammals that part of the allantoic stalk left within the body wall, when the umbilical cord connected with the placenta is severed at birth, enlarges to form the bladder, and also the *urachus*, or *vesico-umbilical ligament* which anchors the bladder to the inner body wall at the umbilicus. Thus the proximal end of the allantois stalk enlarges into the hollow sac of the bladder while the distal part within the body wall under-

goes quite a different fate in being transformed into a solid ligament utilized as a guy rope to support the bladder.

The occurrence of an occasional urachal cyst in man, with urine escaping through the umbilicus by a fistula, apparently demonstrates the embryonic derivation of the urachus and bladder from the common origin of the allantoic stalk.

Arcey * says, however, "Contrary to earlier views, the allantois contributes nothing to the bladder or urachus." According to his view the mammalian bladder is a derivative of the embryonic cloaca. Future studies on this question will be welcome.

The mammalian bladder is lined with mucous membrane and coated on the outside with peritoneum. It has a highly muscular wall abundantly supplied with nerves and blood vessels, the involuntary muscle fibers being diverted from their originally regular, longitudinal and circular arrangement so that they interweave like felt in many directions. Upon contraction the cavity of the bladder becomes smaller, therefore, in all dimensions like a leaking toy balloon, rather than collapsing like a hot-water bag from which the water has been emptied.

The exit from the bladder is by way of a single duct, the *urethra*, the entrance to which is kept closed by a muscular sphincter, except periodically, during *micturition*, when, upon the relaxation of the sphincter, the urine is expelled by the contraction of the muscular walls of the bladder.

There is considerable variation in the location of the points where the ureters enter the bladder. Only rarely, as in *Lepus* and *Hyrax*, do they come in at the opposite pole from the urethral exit as is the case among fishes. In most mammals they enter low down near the urethra by an oblique passage through the wall of the bladder (Fig. 370). This arrangement makes the backflow of urine into the ureters difficult, particularly when the bladder is full, because the pressure from distention tends to close the bore of the ureters.

Both allantoic and cloacal bladders may be attached to the ventral body wall by a remnant of the ventral mesentery, the *ventral ligament of the bladder*, continuous with the visceral peritoneum covering this organ.

* *Developmental Anatomy*, W. B. Saunders Co., pp. 147-8.

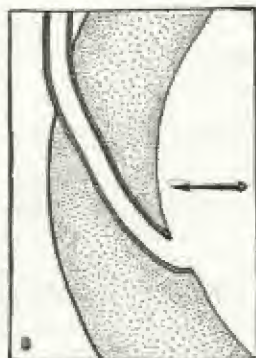


Fig. 370. Diagram of the diagonal passage of the ureter through the wall of the bladder. As the bladder becomes distended the pressure in the direction of the arrow tends to close the ureter.

V. THE SUCCESSION OF KIDNEYS

1. In general

Although all kidneys are fundamentally nephridial tubes that extract liquid waste from the blood, the kidneys of different animals are by no means homologous structures.

Among vertebrates there are three kinds of nephridial structures serving as kidneys that differ from each other not only in structure and position in relation to the blood system and the excretory tubes, but also in their embryonic history.

The three kinds of kidneys, as named by the English embryologist, Balfour, are the *pronephros* of a few cyclostomes; the *mesonephros* of fishes and amphibians; and the *metanephros* of reptiles, birds, and mammals.

The higher vertebrates, whose kidneys are of the metanephric type, pass through preliminary pronephric and mesonephric stages before the per-

manent metanephric stage is reached. As is frequently the case, comparative anatomy and embryology have supplementary and confirmatory stories to tell from different angles about the same thing.

The nearest approach among invertebrates to the vertebrate nephridial apparatus is found in the nephridia of many annelid worms

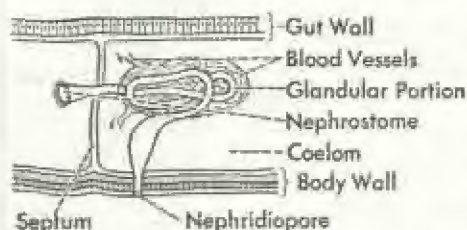


Fig. 371. Diagram of a nephridium of an annelid worm. The anterior end of the animal is toward the left.

(Fig. 371), which, however, are not connected together by common excretory ducts to form excretory organs, like the nephridia of all vertebrates, but rather consist of metamERICALLY arranged pairs of independent tubes.

2. The Nephridial Apparatus of Amphioxus

The nephridial apparatus of amphioxus is very much like that of certain marine annelids (Fig. 372), but instead of extending practically the entire length of the body with a pair of pronephridia in every segment, as in the annelid worms, the primitive *pronephridia* of amphioxus are localized in the anterior part of the body throughout the region of the gill slits. They lie somewhat above the pharynx near the dorsal region and may equal the gill slits in number. Each nephridium is open externally, emptying independently into the peribranchial chamber (atrial cavity) surrounding the

gills, and terminating internally in flame cells of the flagellate type. There are present no common excretory ducts for carrying away the excretion from the nephridia of amphioxus, but the peribranchial chamber, with its atrial opening, accomplishes the same purpose while serving at the same time as the avenue of escape for the water of respiration.

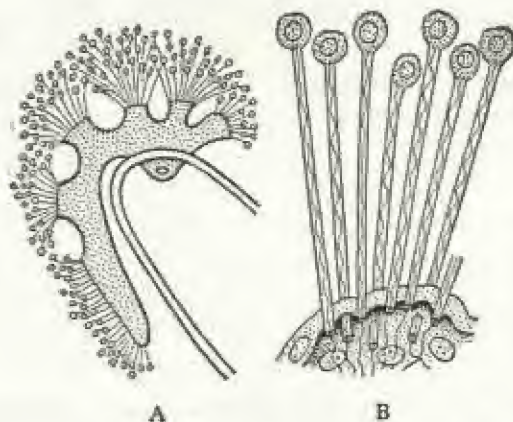


Fig. 372. Excretory tubules of amphioxus. A, a single protonephridium showing several processes, which lie in the coelom, and the single opening, which empties into the atrial cavity; B, one nephridial process enlarged to show the group of flame-cell-like solenocytes, each with a collar and flagellum. (From Newman, *The Phylum Chordata*, copyright 1939, by permission of The Macmillan Company, publishers. Modified from Boveri and Goodrich.)

Thus the apparatus for urinary excretion in amphioxus is primarily concerned with coelomic drainage rather than with direct extraction of urinary waste from the blood, and it consists not of a single pair of organs, or *nephroi*, with their ducts, as in all true vertebrates, but of a series of independent paired excretory tubules of the protonephridial type, resembling those of some annelid worms.

3. Pronephros

The pronephric tubules, *pronephridia*, are few in number and metamerically arranged in the anterior part of the trunk region. Originating as evaginations of the coelomic epithelium along the lateral portions of the mesomeres, or *nephrotomes*, each retains a ciliated mouth, or *nephrostome*, which opens into the *nephrocoele*, the coelomic cavity of this region (Fig. 373). The outer extremities of the pronephridia, ending blindly at first, soon turn posteriorly, growing until they come in contact with one another and

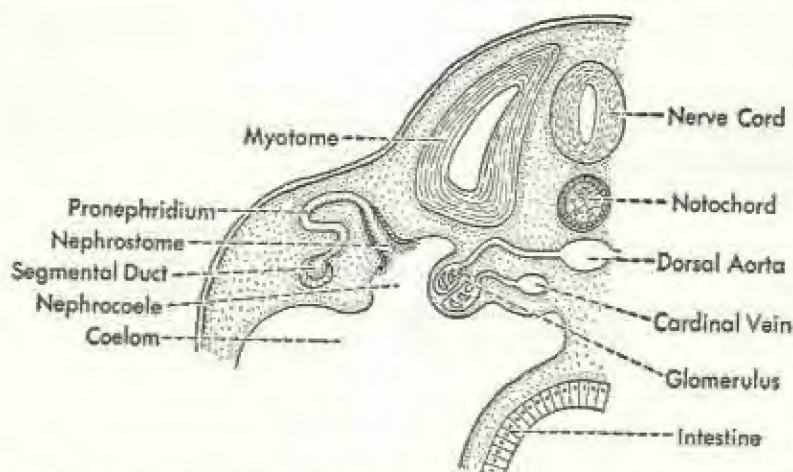


Fig. 373. Cross section diagram showing pronephridial stage of the excretory system. Successive glomeruli frequently fuse into a single, elongate capillary-mass, known as a glomus (See Fig. 374).

join together, down each side of the body, to form a common *segmental*, or *pronephric*, *duct*. This duct is eventually extended posteriorly, mainly by additions from the coelomic wall, to open into the cloaca.

On the opposite side of the nephrocoele from the nephrostomes a capillary ridge, the *glomus*, forms along the coelomic wall (Figs 373 and 374), so that there are two methods of obtaining excretory products from the blood. They can pass first by diffusion into the general body cavity and then into the nephrocoeles or they can go directly from the capillaries of the glomus into the nephrocoele. In either instance the liquid excretory material is passed on through the ciliated nephrostomes and pronephridia to the segmental ducts, which dispose of the waste to the outside.

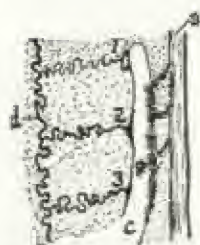


Fig. 374. Reconstruction of the pronephros of *Salamandra*, a, aorta; c, coelom; d, pronephric duct; g, glomus; 1, 2, 3, pronephridia. (After Kingsley; Simon.)

No encapsulating connective tissue, like the tunica fibrosa of the human kidney, surrounds and unifies the pronephridia into a definite organ.

The pronephroi are best developed in cyclostomes, where in some species they persist throughout life, although replaced functionally in most cases by mesonephroi or kidneys of the second order.

It is probable that in some myxinoids, *Polistotrema* or *Bdellostoma*, for example, they remain as the lifelong functional kidneys. They also persist

structurally in some teleosts. In other vertebrates, particularly types like elasmobranchs and amphibians that have a larval development, they put in a temporary embryonic appearance and later vanish.

In the shark *Pristiurus* there are four pairs of pronephric tubules; in the elasmobranch *Torpedo*, six; while in the legless amphibian *Caecilia*, ten pairs of pronephridia hold the stage for a time during early development. Transient traces of pronephridia in mammals have been described, one or more pairs even having been identified in early human embryos where their maximum growth is attained in embryos of about 3.5 mm. in length.

Although the downfall of the pronephridia seems to be universal, with the possible exception of certain cyclostomes already mentioned, the segmental ducts are more persistent and, as will be seen later, are retained to play an important part in the succeeding dynasty of the mesonephros, which reaches its maximum in human embryos of about 10 mm. in length.

4. Mesonephros

The second type of kidney in the vertebrate succession is the *mesonephros*, sometimes known as the *Wolffian body* (Fig. 396). Like other kidneys this structure is made up of nephridial tubules, *mesonephridia* in this instance, that develop in the embryo from nephrotomes posterior to those which form pronephridia and at a later time. They are distinct from pronephridia as shown by their relation to the excretory ducts and by the fact that both pronephridia and mesonephridia may be present at the same time.

Mesonephridia, which are much more numerous than pronephridia, do not generally show the primitive metameric arrangement. The most anterior mesonephridia are the oldest, and subsequent additions arise posteriorly. They originate independently and connect secondarily with the paired segmental ducts that hold over from the former régime (Fig. 375).

Each mesonephridium primarily forks at its inner end. One branch is a ciliated *peritoneal funnel* opening into the coelom, while the other ends in a *Bowman's capsule* associated with an independent glomerulus from the blood system (Fig. 376). Additional capillaries develop about the tube proper somewhat in the same manner as in the case of the mammalian urinary unit previously described. Thus there are established two avenues for excretory collection, namely, the ciliated peritoneal funnel for drawing whatever fluid collects in the body cavity, and the renal corpuscle and tubule proper for direct abstraction from the blood.

In the cyclostomes peritoneal funnels are retained throughout the entire length of the mesonephros, while in some elasmobranchs, ganoids, and

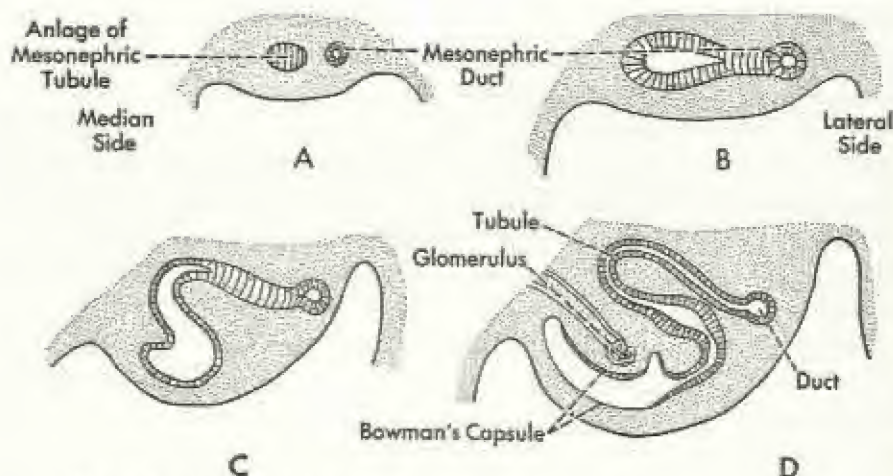


Fig. 375. Diagrams showing the differentiation of a mesonephric tubule (mesonephridium). (After Arey and Felix-Prentiss.)

amphibians the more anterior funnels are the only ones to remain open. In other vertebrates peritoneal funnels are for the most part obliterated.

When all peritoneal funnels disappear, as in most amphibians and in amniotes generally, the body cavity virtually becomes a closed sinus so far as the blood system is concerned, and the peritoneal fluid, with whatever excretory products may be present in it, can escape only like other lymphatic fluids through the blood channels.

The mesonephros functions as the kidney throughout life not only in

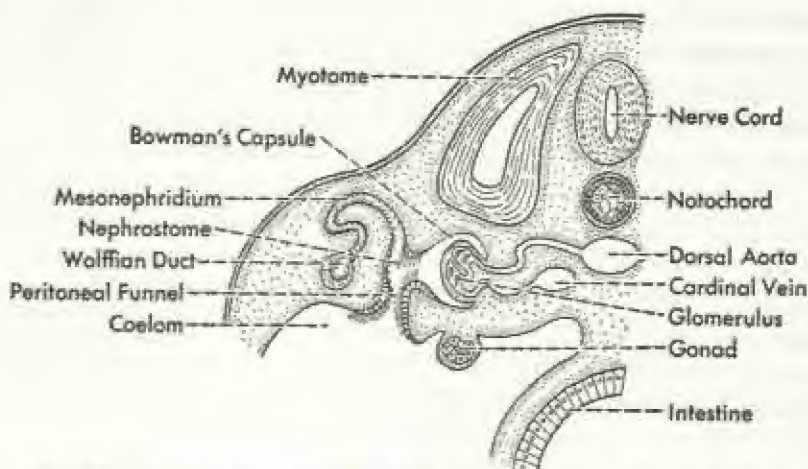


Fig. 376. Cross section diagram showing early mesonephridial stage of the excretory system.

cyclostomes, with the exception of the hagfishes already mentioned that retain a pronephros, but also in fishes and amphibians. It also serves temporarily as the kidney for practically all other vertebrates until it is superseded in turn by the metanephros.

In reptiles, as well as in *Echidna* and *Didelphys* among mammals, the mesonephros endures until some time after birth, and in the case of the lizard *Lacerta*, even until after the first hibernation.

In most mammals the functional mesonephros is confined to the embryonic period, although occasionally, as in the guinea pig and mouse, degenerating so early that it probably never functions as a kidney at all.

In man the mesonephros, or Wolffian body, reaches its high-water mark during the second month of fetal life, when it appears as a slightly projecting ridge on either side along the dorsal part of the coelom from the posterior cervical region to the pelvis, where the two ridges fuse into one.

The drainage ducts of the mesonephroi are the persisting segmental ducts of the vanished pronephroi, known in their new rôle as *Wolffian ducts*. Thus, if the whole mesonephros, whose secretion is delivered through a duct, is compared to a gland, which it certainly resembles in a superficial way, there is one striking difference to be noted between it and an ordinary gland, namely, the duct is formed *before* the secreting part is developed and independently of it.

When in reptiles, birds, and mammals the mesonephros degenerates and gives way to the metanephros, many of its component parts, in particular the ducts of excretion, are salvaged and utilized for other purposes in connection with the reproductive system.

The whole mesonephros, a much more compact and unified organ than its pronephric predecessor, is retroperitoneal, usually fitting snugly against the dorsal body wall, although in amphibia it projects somewhat into the abdominal cavity.

5. Metanephros

The third and last type of vertebrate kidney, which replaces the mesonephros in reptiles, birds, and mammals, is the *metanephros*.

Its nephridial tubules, the *metanephridia*, already described as "urinary units," take their origin in the nephrogenic tissue surrounding the posterior part of the Wolffian ducts in the sacral region of the body, ventral to the sacrum and dorsal to the cloaca when this is present.

The metanephridia are very numerous, elongated, and highly modified histologically, as already indicated. They are not arranged metamerically at any stage, and are massed together inside of the tunica fibrosa so that they

form organs, particularly in mammals, more independent of the coelomic wall than either pronephroi or mesonephroi.

In position the metanephridia are posterior to the last mesonephridia, developing at a later time. A peritoneal funnel is never present, and consequently at no stage do the metanephridia communicate with the coelom. As a result of the absence of the funnel branch of the nephridial tube, the connection with the blood system, that is the renal corpuscle, appears to be at the blind end of the tubule and not on a branch like one arm of a Y, as in the mesonephridium.

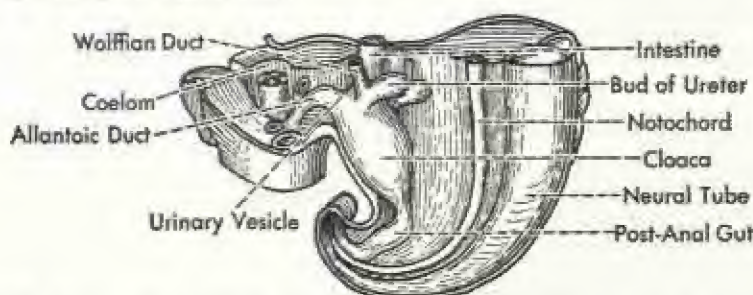


Fig. 377. The cloaca of a human embryo of about twenty-six days, showing beginnings of ureter. (After model by Keibel.)

The true *ureters*, which sprout out from the bases of the Wolffian ducts (Fig. 377), are not made over from something that has gone before, but are an entirely new pair of excretory ducts. The free end of each ureter enlarges and pushes into the metanephric tissue to form the renal pelvis and main collecting tubules of the metanephric kidney. Here again the duct is formed independent of the nephridia but in this case the duct grows to the nephridia instead of the reverse situation which is found in the development of the mesonephros. Meanwhile the Wolffian ducts that have already served more than one master, being shorn of their former excretory mission, are turned over to the reproductive system to take on still another function as sperm ducts in the male, while in the female they degenerate and pass out of the picture.

In man the metanephros, or permanent kidney, assumes dominance during the third month of fetal life. The remains of the mesonephros, as well as the mesonephric ducts, become accessory to the reproductive apparatus later.

In the chapter on the Reproductive System more complete consideration will be given to the fates of all of these ducts and tubules which, although at first urinary in function, become in many cases associated with the genital portions of what is commonly known as the *Urogenital System*.

The Preservation of Species— Reproductive System

I. THE SIGNIFICANCE OF REPRODUCTION

The individual is the triumphant outcome of the age-long interaction of all the mighty and intricate forces of evolution.

The various mechanisms of metabolism thus far considered, including the integumentary, digestive, circulatory, respiratory, and excretory systems, as well as the mechanisms of motion and sensation which are to be described in Part III, all contribute directly to the development and maintenance of the individual. There is indeed only one other concern in nature of greater moment than the up-keep and well-being of the individual and that is the continuation on the face of the earth of those precious products of evolutionary travail which have "won a place in the sun." *Life must go on.* Such is nature's ultimatum, although no single individual, even of the genus *Homo*, is of so supreme importance that it cannot be spared. Individuals die only to be replaced by others, and in the long run this is a fortunate provision, since it is the fate of every organism, like any other delicate piece of machinery, to wear out and become useless eventually in the natural course of events.

To provide for the *life of the species* by replacement is the part of *reproduction*.

Filling the gaps caused by the death of individuals in the rank and file of organisms may be regarded as a matter of *extra growth beyond individual requirements* at the expense of non-living materials. The surplus thus gained may become detached from the original organism to form a new and independent individual. Excess growth material endowed with the capacity to reconstruct a new individual is termed *germplasm*, while the body from which it is detached is composed of *somatoplasm*.

Organisms generally, which are made up of these two kinds of materials,

consequently lead a dual life. The mortal somatoplasm is inevitably headed towards eventual death, while the potentially immortal germplasm has opened up before it the possibility of escape from death through reincarnation in a new individual life.

The germplasm thus forms a *continuum* which joins generations together. Any particular organism represents not something new, like a manufactured article, but the ultimate link in an unbroken chain extending back into the evolutionary past farther than the imagination can follow it. In this way the torch of life is not extinguished but is handed on.

Maintenance of the species, as contrasted with maintenance of the individual, is an unselfish altruistic function, frequently accomplished at the expense of individual comfort, or even at the sacrifice of the individual life.

The effective operation of the function of reproduction on the part of animals lacking the ability to reason and uncontrolled by altruistic motives is insured by being grounded firmly in fundamental urges and universal desires which carry the reward of selfish satisfaction while at the same time accomplishing the altruistic end of providing for others.

That flower of creation, *moral man*, in spite of the fact that he is by no means entirely emancipated from the effective laws of the jungle, has in comparatively recent evolutionary times set up certain ethical rules to govern the operation of the indispensable function of reproduction that are somewhat at variance with a life of selfishness. Moral responsibility does not worry animals.

It is perhaps biologically fortunate that man, although subjected to an overlay of social restraints, is still bombarded by the same universal compelling physiological urges with their rewards of selfish gratification which serve to safeguard and insure the altruistic and sacrificial ends that result in the perpetuation of the species.

II. METHODS OF REPRODUCTION

Sex, in spite of the popular impression to the contrary, is not essential to reproduction. Many organisms reproduce their kind *asexually* by processes of unequal fragmentation, such as budding and spore formation, or by more or less equal division into two, as in the fission of many protozoans.

The first event in the life of any vertebrate, however, is the union of two highly endowed cells, called *gametes*, furnished by two different individuals, male and female. The undifferentiated cell thus formed is a "fertilized egg," or *zygote*, than which no other cell has so great expectations.

This is *sexual reproduction* and in describing the mechanism involved

one should first of all distinguish the essentially "immortal germplasm" (Weismann) that bridges the generations, from the accessory structures which minister thereto, but are destined to perish with the life of the individual of which they form a part.

III. THE ESSENTIAL REPRODUCTIVE CELLS

Germplasm, the essential material concerned in reproduction, consists of sperm cells and eggs in sexual animals.

1. Sperm Cells

The detachable germinal units derived from the male individual are *sperm cells*. They are frequently called *spermatozoa* (*sperma*, seed; *zoön*, animal), an awkward and misleading word, embalming the historical fact that when these cells were first discovered by early microscopists, they were thought to be tiny independent parasitic animals.

A sperm cell in order to produce a new individual must always join forces with an egg cell. It can never become an individual unassisted. Such union, however, is not indispensable in the case of the egg cell, which among certain invertebrates may develop parthenogenetically, that is, without the assistance of a male sperm cell.

The sperm cells of different species have a *chemical specificity* for the eggs of their own kind, and animals do not bastardize under ordinary conditions even though their germ cells may have free access to each other, as in sea-water for example, where a variety of different kinds of eggs and sperm are present. If this were not true, untold confusion would result.

The *motility* which enables the active sperm to seek out the comparatively stationary egg is accomplished among vertebrates by the development

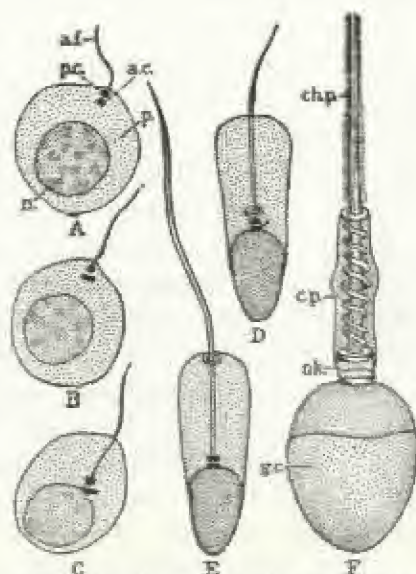


Fig. 378. Diagrams of the development of spermatozoa. *a.c.*, anterior centrosome; *a.f.*, axial filament; *c.p.*, connecting pieces; *ch.p.*, chief piece; *g.c.*, galea capitis; *n.*, nucleus; *nk.*, neck; *p.*, protoplasm; *p.c.*, posterior centrosome. (From Bremer and Weatherford, *Lewis and Stöhr's Histology*, copyright 1944, by permission of P. Blakiston's Son and Company, publishers. After Meves.)

of a vibratile "tail," that sculls the cell body of the sperm forward through a liquid medium. Certain invertebrates, however, such as some of the nematode worms, arachnids, mites, myriapods, and many crabs, have amoeboid sperm cells which creep to their destination in contact with a substrate instead of swimming freely through an intervening fluid. Fish sperm do not take on an independent motility until they are expelled into the water.

The details of *structure* of a typical sperm, together with an indication of the sequence of events by which it attains a highly specialized locomotor form from its generalized embryonic shape, are shown in Figure 378. Cockrell has happily described a mature sperm cell as stripped "like a Roman soldier without impedimenta." Its entire cytoplasm, indeed, is sacrificed to forming a structure devoted to carrying forward the "head" of the sperm, which is practically only the nucleus containing the chromosomal bearers of heredity.

The *numbers* of sperm cells produced by male animals of different species is greatly in excess of the number of eggs furnished by corresponding females. It has been estimated by Shipley that in man, for instance, the total number of sperm cells produced during the sexual life may be 340 billion, while the eggs that come to maturity during the lifetime of a human female will hardly exceed 400. This makes the ratio of possible sperm to eggs in humankind something like 850,000,000 to 1.

There is a corresponding discrepancy in *size* between the male and female germ cells, yet it is a demonstrated fact that the egg and sperm are essentially equal partners with respect to hereditary chromosomal determiners which each sex contributes to the mutual enterprise of a new individual.

The *viability* of sperm cells after detachment from the male likewise shows great variation. Haempel gives the duration of independent life in water of the sperm of certain fishes, as follows:

<i>Trutta fario</i>	23 seconds
<i>Trutta viridea</i>	40 "
<i>Trutta salar</i>	45 "
<i>Salmo hucho</i>	45 "
<i>Barbus fluviatilis</i>	120 "
<i>Esox lucius</i>	3-4 minutes
<i>Cyprinus carpio</i>	5 "

According to Lewis, human sperm may retain activity for three days after the death of the male, and if deposited in the female genital tract, for a week or more.

The sperm of some bats remain alive and efficient from the time of

pairing in autumn until the following spring, when the eggs are ready for fertilization. Among invertebrates may be cited the remarkable case of the honey bee, where the sperm from the drone may live in the body of the queen for over a year.

2. Eggs

The *ova*, or germplasmal cells of the female, are less independent of the individual which produces them than the sperm cells of the male. In many instances they tarry within the protective body for a considerable time after attaining potential independence and may even undergo extensive development into a new organism, as for instance in mammals, before forsaking the maternal body in which they originated.

The fact that an egg is "fertilized" by sperm and not *vice versa* has entailed the necessity for providing various additions to the egg cell itself in the form of stored nutrition and protective envelopes for the forthcoming individual that are entirely unnecessary in sperm cells. The chief emergency ration stored in the egg is *yolk*, which represents one of the earliest instances of "preparedness" on record. The quantity of such food in the eggs of different species of animals varies all the way from a meager fat droplet in certain protoplasmic eggs to the relatively enormous supply making up the familiar yellow sphere in a hen's egg. The large size of the latter is due to the generous supply of stored food material and not to the amount of living cytoplasm which is little different from that of much smaller eggs.

In addition to yolk, the eggs of turtles, crocodiles, and birds have a supply of albumen, or "white," wrapped around the yolk that adds variety to the embryonic bill of fare.

The eggs of amphibians also are covered with a glairy albuminous coating, which has the property of swelling up into a thick protective jelly-like envelope upon exposure to water (Fig. 379). This explains why the total quantity of eggs which a submerged frog or toad lays all at once, enlarges and floats to the surface, forming a mass considerably greater than that of the entire body whence it came. The eggs of toads are strung together like pearls, while those of frogs and salamanders are in gelatinous clumps.

Eggs that are not shed directly into water, or do not undergo preliminary development into embryos within the sheltering body of the female, are provided with some sort of a protective *shell*. This may be leathery or of a texture like parchment, as in many reptiles, but it is usually calcified, being



Fig. 379. A bunch of frog's eggs attached to a stick. (After G. H. Herrick.)

perforated by innumerable tiny air holes through which respiration takes place. The calcareous-shelled egg of the warm-blooded bird differs from that of the cold-blooded reptile by having: (1) a heavier firmer shell; (2) an air chamber at one end within the shell (Fig. 380); and (3) a greater amount of supplementary albumen, a part of which develops into the *chalaza*, that anchors the yolk at either pole like a twisted guy rope, preventing undue mechanical disturbance.

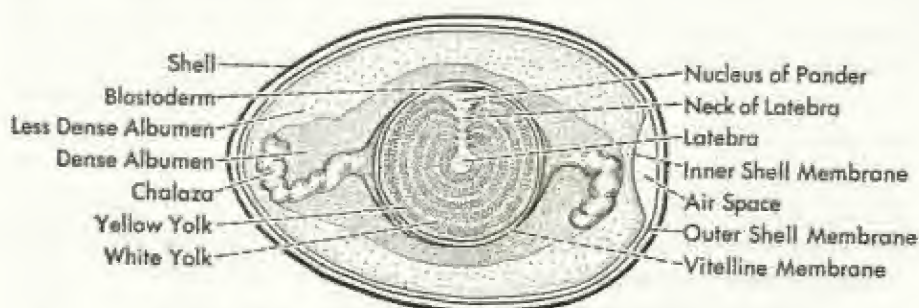


Fig. 380. Egg of a bird (After Schimkewitsch.)

The *chalaza* also allows the yolk, bearing its precious protoplasmic disc, to rotate within the shell so that the disc is always on top and not pressed against the shell, regardless of the position of the egg as a whole. All of these additional modifications of the avian female germ cell are devices called forth by the necessity of egg-laying on land and subsequent incubation.

After an egg has taken in a sperm and is "fertilized," it requires a period of enhanced temperature in order to begin development into an embryo. This is the period of incubation. Fishes usually resort to warmer waters to spawn and turtles deposit their eggs in sand where the heat of the sun has access to them. Sea turtles, whose young are liable to greater hazards than land turtles, come ashore and abandon on the friendly doorstep of sand and sun as many as 150 or 200 eggs, while alligators pile up a swampy nest of rotting vegetation in which to leave their eggs, the fermenting mass engendering the amount of added heat requisite for bringing the eggs to the hatching point. Frogs' eggs, deposited in the shallow water along the margins of ponds in spring, receive the sun's rays through their transparent spherical jelly-like envelopes which act like a lens in focusing the heat, thus providing the necessary increase in temperature. Birds build incubators in the form of nests where the temperature of their eggs is raised by means of contact with the warm bodies of the parents.

In *shape* the eggs of vertebrates are typically spherical, particularly those

of fishes and amphibians that are deposited in water, as well as those of mammals which do not require a shell because they are not exposed. The eggs of reptiles are usually elongated and elliptical, while those of birds are prevailingly oval with one end more pointed than the other so that they pack economically within the confines of a nest. Most sea birds build shallow nests, depositing their eggs either in perilous crevices or in flat exposed situations, consequently their eggs taper so much that they do not roll away when disturbed, but simply pivot about in a circle, remaining safely in the nest.

As already pointed out, the egg by reason of the presence of yolk and albumen exceeds the sperm many times in size. The human egg (Fig. 110) is very small, but although only about $\frac{1}{125}$ of an inch in diameter, it is nevertheless 50,000 times larger in volume than a single sperm, which measures scarcely 5 micra in diameter.

The eggs of marine fishes are usually smaller and more numerous than those of fresh-water fishes, although elasmobranchs form a notable exception, as they have the largest eggs not only of any fishes, but also probably of any animal. Braus reports a specimen of the shark *Hexanchus griseus* that measured 4.2 meters in length and weighed 400 kilograms, from which he took out of a single oviduct 53 eggs of approximately the same size, each measuring 9 by 11 centimeters and weighing about 500 grams. The eggs of certain Japanese carcharid sharks are known to attain the size of 14 by 22 centimeters, dimensions considerably exceeding the average of 12 by 15 centimeters common to ostrich eggs.

The number of eggs produced bears a direct relation to the chances for attaining maturity. Elasmobranch fishes, the young of which are born alive and well advanced at birth towards a stage when they can fend for themselves, produce only a few eggs (Fig. 381). Prevost, for instance, gives four to fourteen ova as the seasonal output of the elasmobranch *Torpedo marmorata*. The stickleback, *Gasterosteus*, which makes a nest that is guarded by the male, lays less than a hundred eggs. On the other hand the codfish, *Gadus*, whose unprotected eggs are exposed to the countless perils of the open ocean, broadcasts several million eggs during a single

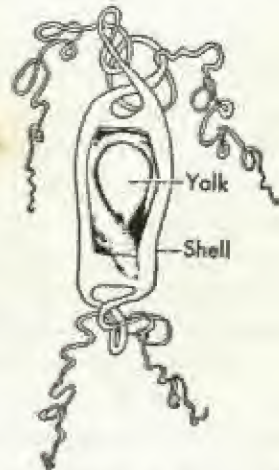


Fig. 381. Egg case of *Scyllium*, a dogfish, cut open to show the embryo surrounding the yolk within. The egg case is prolonged into entangling tendrils. (After Hume.)

breeding season. This enormous output in turn is numerically low when compared to that of certain termites among the insects whose queen lays eggs continuously at the rate of one per second for a year at a stretch, making a total of some 30 millions from a single female.

Ascending the vertebrate scale from fishes through amphibians (Fig. 28), reptiles, and birds to mammals, there is an increasing provision for parental care with a corresponding falling off in the number of eggs produced that suggests the mathematical computations and conclusions of an expert life insurance actuary.

When eggs are supplied with a large amount of yolk, the embryos have the opportunity to reach a more advanced stage of development before hatching, but in the case of poorly provisioned eggs they must embark on their worldly adventures with less preparation. Mammals, whose eggs are practically devoid of stored nourishment, attain the advantages of advanced preliminary development by the device of gestation.

IV. SECONDARY REPRODUCTIVE APPARATUS

As already indicated, eggs and sperm are the essential reproductive cells. They preserve and carry forward the architecture and traditions of each species, but in doing this they require a place of abode, devices for bringing the germ cells together in effective union, and provision for the safe development of the fertilized egg into a new individual. These aids to the germplasm are a part of the *somatoplasm* (Weismann), or the non-germinal body of the individual. From the viewpoint of the species the body, or somatoplasm, may be regarded simply as a mortal vehicle for temporarily maintaining and transmitting the immortal germplasm.

The parts of the body that are in the direct service of the germ cells are (1) gonads, or organs that house eggs and sperm; (2) ducts, or passageways that transmit the germ cells; (3) apparatus of various sorts for facilitating the union of the sex cells; (4) accessory glands; (5) devices for the care of the eggs before and after fertilization; (6) certain rudimentary organs of doubtful utility; and (7) modifications of the body that differentiate male from female, and which may possibly influence sexual behavior.

1. Gonads

The gonads are paired masses of mesodermal tissue (Fig. 382) that develop on either side of the mesentery in the antero-lateral part of the vertebrate body cavity. They become invaded by potential germ cells which,

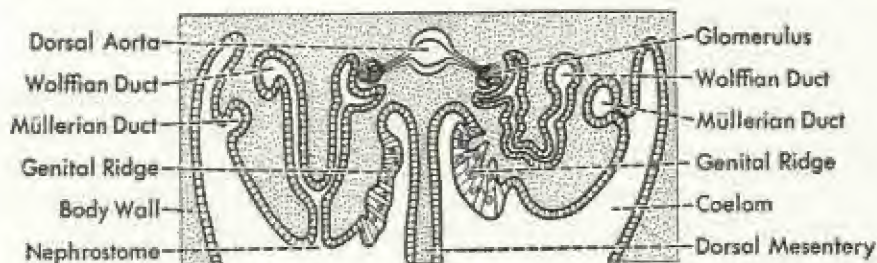


Fig. 382. Diagrammatic cross section across the Wolffian and genital ridges, to show the origin and relations of the Müllerian ducts and tubules of the Wolffian body. (After Pasteau.)

like all other cells, are the direct lineal descendants by mitosis of the original fertilized egg from which the organism arose (Fig. 383). They differ from other cells of the body in retaining their undifferentiated condition for a longer time.

Gonads that harbor future sperm cells are called *testes*, and those in which egg cells are embedded, *ovaries*. According to an almost universal rule among vertebrates, the testes and ovaries develop in different individuals, that is, the sexes are distinct from each other.

Usually gonads are massive structures that do not show metamerism, but in amphioxus they are arranged metamerically along the gill region in as many as twenty-six pairs. The largest pairs are in the middle with others decreasing in size at either end. Although superficially alike, the sexes are distinct.

In most vertebrates, however, there is not more than a single pair of gonads, and consequently metamerism or segmentation, so characteristic of many organs, disappears. In a few vertebrates only a single gonad is present, either as the result of the fusion of a pair as in the lamprey eel, or of unilateral degeneration, as in the hagfish, and the single left ovary of most birds, while frequently one of a pair of gonads will be smaller than its mate.

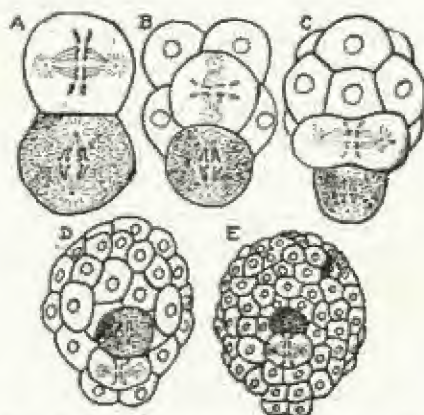


Fig. 383. Separation of somatic and germplasmal cells in five stages in the developing embryo of the nematode worm, *Ascaris*. The darkened cells represent the germplasm, becoming in *a*, the ancestral cells from which the eggs or sperm arise. All other cells by repeated division become the body of the worm. (After Meisenheimer.)

The germ cells, the distinctive features of gonads, arise from embryonic endoderm and migrate into the genital ridges.

The shape of gonads is in general influenced by the body form of the animal to which they belong. Thus, in the wormlike amphibian, *Epicrinum*, they resemble a segmented chain; in urodeles they are long and spindle-shaped, and in frogs and toads, oval. Among reptiles it is easy to distinguish the gonads of the short wide turtles from those of elongated snakes by shape alone.

During the breeding season gonads, particularly those of the prolific fishes, increase enormously in size with the multiplication and growth of the germ cells. The gonads of males are always more compact organs than those of the corresponding females because of the difference in size of the germ cells that are contained in them.

(a) **Testes.**—The *testes* (*testis*, witness) are so called because in former times hands were placed on these important organs when "testifying" under oath.

They not only harbor sperm cells but also produce internal secretions, or *hormones*, which are concerned with the development of the so-called *secondary sexual characters* that differentiate a male in appearance from a female.

A testis arises as a *genital ridge* along the ventro-medial border of the mesonephros, or *Wolffian body* (Fig. 382). In most of the lower vertebrates it maintains an intimate relation with the anterior part of the mesonephros, that in this region loses its original excretory function, becoming transformed into a useful accessory reproductive organ, the *epididymis*, through which the sperm pass on their way to the sperm duct. Even higher up among mammals the epididymal portion of the transient mesonephros is still preserved as an integral part of the reproductive apparatus in the male. The entire structure becomes rudimentary in the female mammal, being represented only by useless fragmentary remains that, like degenerating organs generally, are frequently the focus for cystic formations and other pathological troubles.

Both blood vessels and nerves reach the testis between layers of tissue continuous with the peritoneum, thus forming the *mesorchium*, which serves as an anchoring bridge between the body wall and testis in the same way that the mesentery serves the intestine.

Teleost fishes form a notable exception with respect to intimate dependence of the reproductive organs upon the nephridial apparatus, for in them the testis is entirely emancipated from the mesonephros, with no attendant epididymis.

The compact testes of mammals are generally somewhat oval bodies, enclosed in a close-fitting capsular sheath of connective tissue, the *tunica albuginea*, outside of which, on the free exposed surface at least, is a layer of mesothelium, the visceral layer of the *tunica vaginalis*, homologous with the peritoneum that lines the body cavity. Underneath the tough tunica albu-

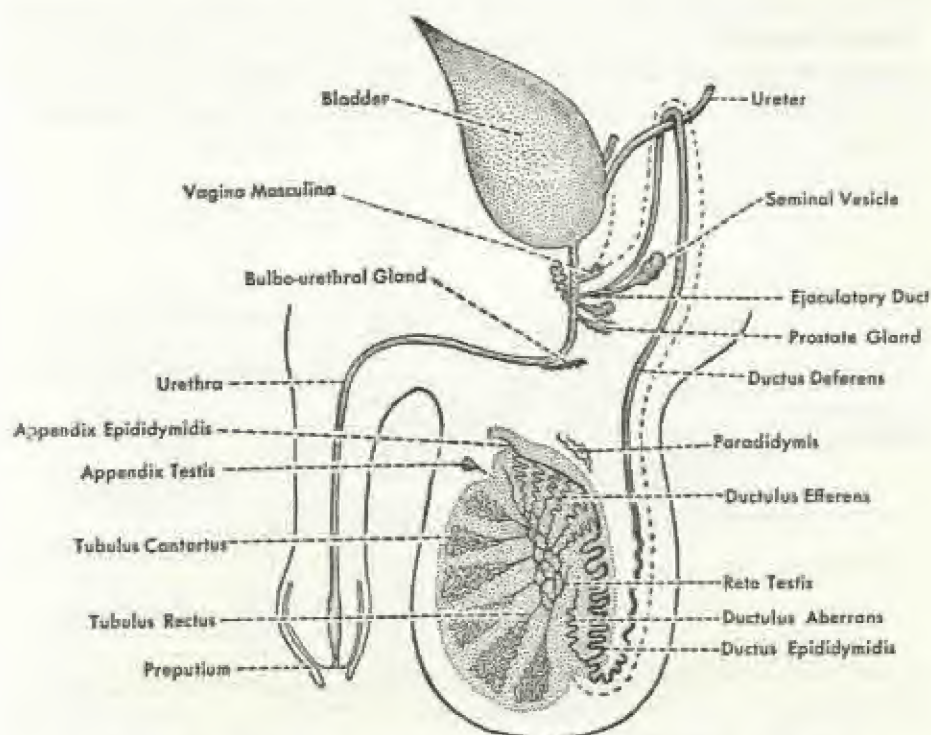


Fig. 384. Diagram of the male sexual organs. The course of the Müllerian duct is shown by the broken line. The course of the ductus deferens is schematized; in its actual course anteriorly, it runs ventral to the symphysis pubis which would be at the left of the diagram near the base of the penis. (From Bremer and Weatherford, *Lewis and Stöhr's Histology*, copyright 1944, by permission of P. Blakiston's Son and Company, publishers. After Waldeyer.)

ginea is another layer of looser texture well supplied with blood vessels, the *tunica vasculosa*. Partitions of connective tissue extend from the tunica albuginea from one side to the other, dividing the whole testis into wedge-shaped compartments (Fig. 384) within which are lodged the *seminiferous tubules* that produce the sperm cells (Fig. 385). Two sorts of cells are found within the walls of these tubules; first, the supporting and possibly nutritive

Sertoli cells; and second, the primordial germ cells, or *spermatogonia*, destined after repeated mitoses to give rise to the sperm.

Between the tubules there are blood vessels, and still another kind of cells that form the endocrine part of the structure, namely, *interstitial cells*, or the so-called "puberty glands" of Leydig.

In man the seminiferous tubules (Fig. 384), of which there may be several hundred, are very much kinked-up for the most part of their length (*tubuli contorti*), but they straighten out (*tubuli recti*) as they focus together at the inner side of the testis. A single convoluted tubule, occupying ordinarily a span of not more than one inch, stretches out when uncoiled to over a foot in length.

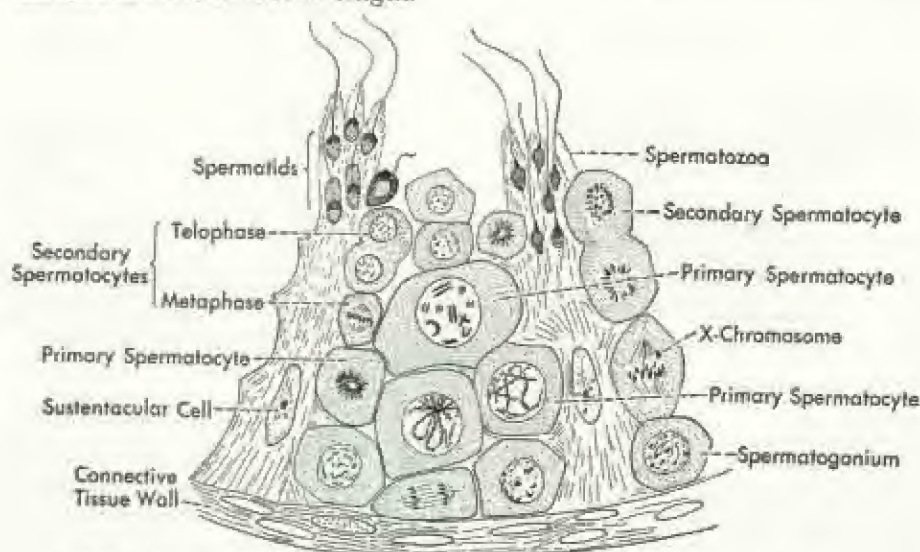


Fig. 385. Stages in the spermatogenesis of man, arranged in a composite to represent a portion of a seminiferous tubule that has been sectioned transversely. (After Arey.)

Tubuli contorti pass over continuously at their inner ends into tubuli recti which anastomose together into a network of tiny passages forming the *rete testis*, from which emerge other continuous tubules, *ductuli efferentes*, that pass through the epididymis, eventually reaching the sperm duct, or *ductus deferens*, leading to the outside.

The original anterior embryonic position of the testis within the body cavity is by no means always maintained. There is an evolutionary tendency, particularly among mammals, for the testes to migrate backward during the course of development. In the higher animals this tendency is carried to so great an extreme that the testes forsake the protection of the body

cavity entirely and come to hang outside in a sac of outpushed skin and muscle known as the *scrotum* (Fig. 386).

According to the degree of migration which the testes have undergone, animals in general may be separated into three groups as follows: first, those in which the testes remain within the confines of the body cavity; second, those in which there is a temporary descent during periods of sexual activity, followed by a withdrawal into the body cavity; and third, those with a permanent descent into the scrotum. To the first group belong all vertebrates below the mammals, and among mammals, monotremes, many insectivores, coneys, elephants, and whales. In the second group are many rodents, some insectivores, civet cats, otters, llamas, bats, camels, and certain apes. Those with a permanent descent of the testes after the fetal period, include marsupials, pinnipeds, and most carnivores, ungulates, and primates.

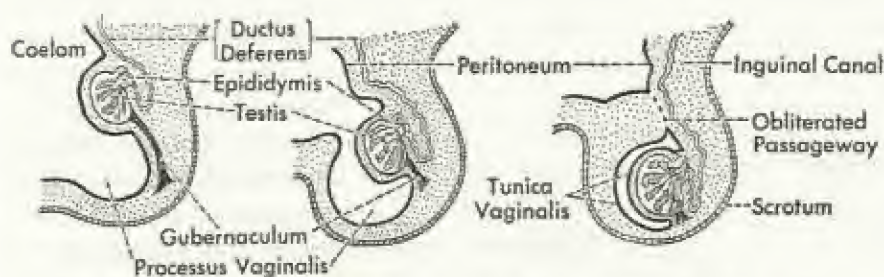


Fig. 386. Three stages in the descent of the testes. (After Patten.)

The testes lie within a cavity in the scrotum which is homologous with the body cavity of which it was originally a part. As a result of this peculiar development there is a double layer of enwrapping peritoneum, or tunica vaginalis, about the testes, one the *parietal layer* lining the scrotal coelom itself, and the other the *visceral layer* which is reflected over the surface of the testes in close contact with the tunica albuginea, as already mentioned.

The *inguinal canal*, a continuous passage-way between the abdominal cavity and the scrotal sac, remains open in those mammals subject to a temporary descent of the testes. It is always pervious also in marsupials, although in other mammals having a permanent descent it ordinarily becomes closed. Through it runs the *spermatic cord* composed of arteries, veins, lymphatics, and nerves in addition to the ductus deferens itself. As in the case of all abdominal organs, the testis and these structures in the inguinal canal are all extra-coelomic, i.e., outside the coelom.

The wall of the scrotum is essentially the same as the neighboring body

wall except that the skin is more highly pigmented and has a looser subcutaneous layer, and a greater supply of smooth muscle cells than the skin of other parts of the body.

In man the descent of the testes ordinarily occurs shortly before birth. Instances occur where the testes are abnormally retained within the body cavity, resulting in cryptorchism (*cryptos*, hidden; *orchis*, testis), but this unusual state of affairs has a perfect explanation in the light of comparative anatomy. The tapir and rhinoceros have no pendulous scrotum, although the testes leave the body cavity and come to lie in pockets close under the skin. A similar anomalous condition is seen in some flatfishes (Pleuronectidae), in which not only the testes but also the ovaries are crowded out of the cramped quarters of the body cavity and find a haven in pockets "extending backwards into a kind of concealed scrotum between the integument and muscles on each side above the anal fin." (Owen.)

Why the testes of the highest vertebrates, with their precious contents, should push out the body wall into a scrotal sac and hang over the edge of the pelvic bones in so exposed a situation is not at once apparent. Certainly the outpushing of the body wall by the protruding testes leaves centers of structural weakness that entail liability to hernia and frequent attendant troubles. Studies by Moore and others seem to indicate that temperature as high as that normally maintained within the mammalian body is somewhat detrimental to the functioning of spermatozoa. The descent into the scrotal sac is a device whereby the testes are exposed to a lower temperature than that within the body cavity, thus favoring the development of the sperm. In the case of animals having a temporary descent of the testes there is delayed development of the sperm while the testes are retained within the body cavity. This theory also accounts for the frequent sterility that accompanies cryptorchism. It does not explain the production of sperm by avian testes, located in the body cavities of animals maintaining higher bodily temperatures than do mammals.

(b) **Ovaries.**—Ovaries, like testes, arise as genital ridges and are "glands" of double function, producing cells, or *ova*, and endocrine secretions that are distributed through the blood. They may be simply attached to the peritoneum, or encapsuled when they hang freely in the body cavity, being connected to the body wall by a *mesovarium*, homologous with the mesorchium of the testes. They may also be embedded in the peritoneum, as in the rabbit and cat.

Asymmetrical development of the ovaries appears in some elasmobranchs, particularly of the families Trygonidae and Myliobatidae, where the right ovary is forced to make way for the intestine with its extra large

bulky spiral valve. Some of the bony fishes, for example the perch *Perca*, and the curious little sand-lance *Ammodytes*, show a fusion of the two ovaries into one, while in *Mormyrus oxyrhynchus* of the Nile, and some others, only the left ovary develops.

In birds also only a single ovary develops (Fig. 387), the left one being the one that is "left," although a few birds, such as owls, hawks, pigeons, and parrots sometimes show remains of the lost right ovary.

The advantage resulting from the single ovary in birds may have to do with the drastic elimination of unnecessary ballast in adaptation to flight, or possibly with the safe manipulation of large eggs with breakable shells. Only a single oviduct remains when there is a single ovary, but in the case of two ovaries and two oviducts it might well prove disastrous if two eggs with fragile breakable shells should approach the narrow exit side by side at the same time.

Ovaries of elasmobranchs, crocodiles, turtles, birds, and mammals are more or less solid in character, and the eggs that are embedded in them dehisce through the periphery directly into the body cavity to be picked up by the open ends of the oviducts.

Amphibians, lizards, and snakes have saccular ovaries which are hollow within, but the eggs still break through the outer walls, arriving in the oviducts by the indirect coelomic route.

The ovaries of many teleost fishes, that are likewise hollow, form an apparent exception. In this case the eggs collect *within* the ovaries and pass directly into an *ovarian sac* from which an oviduct conducts them to the outside without their entering the body cavity at all. As a matter of fact the space within the ovaries and that within the sac are both actually shut-off portions of the original body cavity (Figs. 388 and 389). The ovarian sac, formed when the ventral free edge of the genital ridge grows laterally to join the body wall and close off a portion of the body cavity, extends posteriorly to attach to the anterior end of the short oviduct and provide an independent communication between the sac and the outside. In several families of teleosts, in which these sacs do not develop, the eggs are shed into the main body cavity from which the oviducts carry them to the out-

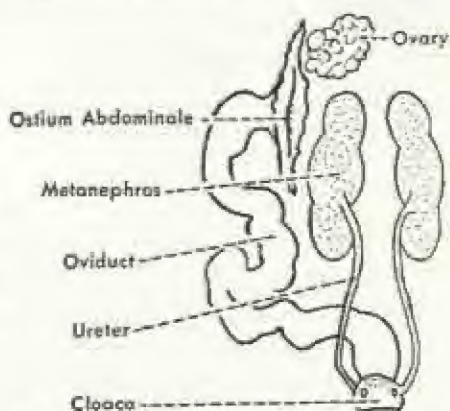


Fig. 387. Urogenital organs of a female bird showing the single left ovary from the dorsal side. (After Roule.)

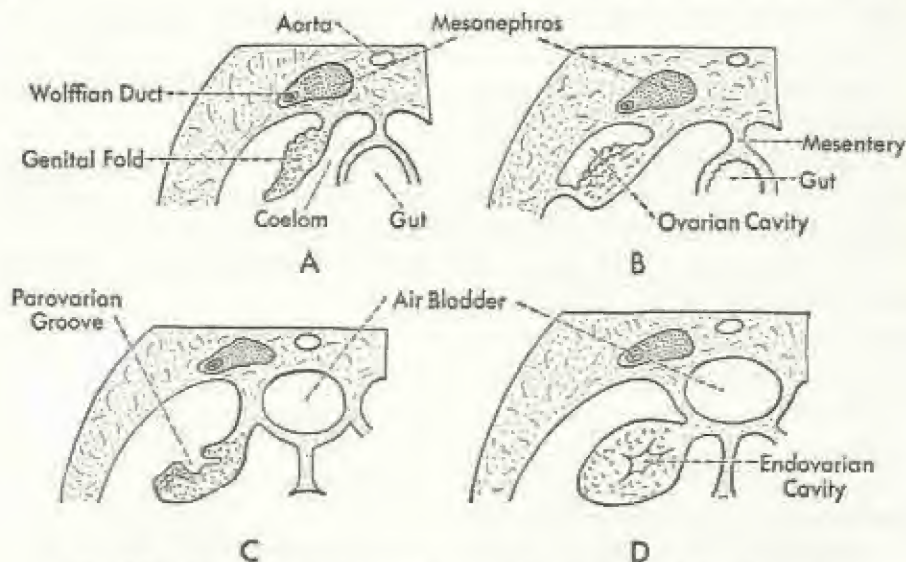


Fig. 388. Diagrammatic sections showing development of closed ovaries. A and B, *Cobitis*; genital fold free in A, but fused to coelomic wall in B. C and D, *Aeterna*; ovary open in C, and closed so that groove becomes internal cavity in D. (A and B, after Schneider; C and D, after Jungersen.)

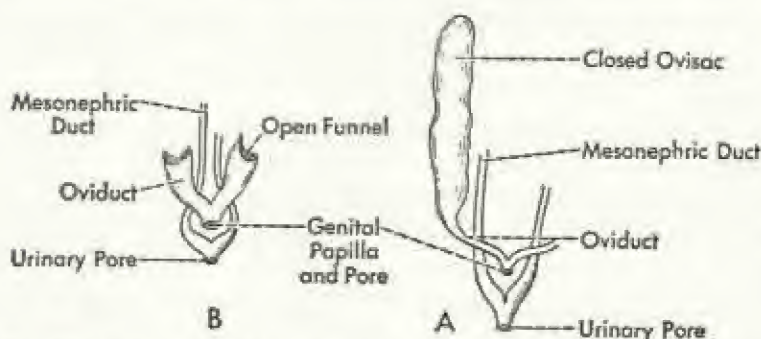


Fig. 389. Diagrams of female urogenital ducts in teleosts. A, a teleost with a closed ovisac; B, one with a short oviduct opening into coelom by a large funnel. (After Goodrich and Weber.)

side. In all of these cases it is clear that the eggs are inducted into the body cavity on the way to the oviduct.

The garpike, *Lepidosteus*, alone of the ganoid fishes follows the teleost plan. Other ganoids have open oviducts and "solid" ovaries.

During the breeding season the ovaries of fishes become engorged with eggs and increase enormously in size, until they may equal as much as twenty-five or thirty per cent of the total body weight.

The cavity of the saccular amphibian ovaries is lymphoid in character and is not comparable with that of teleosts from which it differs fundamentally in origin, its lumen having been hollowed out secondarily instead of representing a portion of imprisoned body cavity.

In turtles the ovaries are symmetrically disposed, but asymmetry in position appears in lizards and becomes quite pronounced in snakes, with the right ovary placed in advance of the left.

The ovaries of the duckbill, *Ornithorhynchus*, owing to the few large projecting eggs which they contain, are somewhat lobulated, "resembling a bunch of grapes," while those of most other mammals are relatively small, round, and smooth in contour, being enveloped in a dense layer of fibrous tissue, the *tunica albuginea*. Underneath this layer is the *cortex*, which is the general seat of the ova, while the interior tissue constitutes the *medulla*, or vascular region of the ovary.

(c) **Hermaphroditism.**—By far the greatest number of all vertebrates are *dioecious* (*di*, two; *oikos*, house), that is, the ovaries and testes are borne by different individuals. There are a few instances, however, of *hermaphroditism*, when the two sexes (*Hermes* and *Aphrodite*) are combined in a single individual, a condition not uncommon among invertebrates, that by reason of isolation or absence of locomotor organs need to overcome the difficulties attendant upon pairing. For example, the sea bass, *Serranus scriba*, is regularly hermaphroditic and self-fertilizing, while another exceptional teleost, *Chrysophrys auratus*, is reported as a protandrous (*prot*-, first; *andr*-, male) hermaphrodite, being "first male" and afterwards female.

The unpaired gonad of the hagfish *Myxine*, appears at times to produce sperm, and at other times eggs, while the larval ammocoetes form of the lamprey eel, according to Lubosch, shows hermaphroditic gonads in twenty-five per cent of the cases.

Occasional hermaphroditism has been observed in codfish, mackerel, and herring among bony fishes, as well as in the Alpine newt, *Triton*, and in frogs and toads among amphibians.

Instances of so-called human hermaphrodites, cited in medical literature, usually refer to abnormalities of the external genitalia rather than to functional gonads. It is extremely doubtful whether there is any authentic case on record of a human being that has produced both eggs and sperm, since the evidence in supposed instances tends to be extremely obscure.

(d) **Gametogenesis.**—The fertilized egg of any vertebrate, when ready to give rise to a new individual, is composed of germplasm laden with the hereditary potentialities of the species to which it belongs. By a succession of innumerable mitoses this original cell soon becomes a mass of daughter

cells from which the somatoplasm, or the body of the individual, is elaborated. Somewhere early in the series of cell divisions there comes a parting of the ways between reserve germplasm and somatoplasm, whereby one of the two cells resulting from a mitotic division is set aside to carry on the traditions of the race, while the other continues in the service of the developing individual (Fig. 383). Each of these two kinds of ancestral cells, particularly that of the somatoplasmic line, undergoes countless subsequent mitoses, with the result that the two lines come to differ fundamentally according to the purpose for which they are destined.

The germplasmal cells find sanctuary in the gonads where they remain practically unchanged until puberty, that is, until the time when the individual that holds them in trust arrives at sexual maturity. They then awaken into activity, following the prolonged dormant period, and by a series of transforming changes become *mature* sperm and eggs, fit for union into a zygote or fertilized egg. This process of preparation is called *gametogenesis* (*gamete*, marrying cell; *genesis*, origin).

The essential process in the final differentiation of the sexual germ cells is the elimination of half of the chromosomal material bearing the hereditary potentialities from the nucleus of the egg or sperm, so that upon the union of the two germ cells the number of chromosomal units proper and characteristic for the species in question will be restored. This *maturation process* has been described in Chapter VI. If this *reduction of the chromosomes* did not occur before the fertilization of the egg, there would be a doubling of chromosomes in each generation which would inevitably upset the necessary machinery of mitosis.

The transformation of *spermatogonia*, or primordial sperm cells, into mature locomotor sperm having half the original chromosomal contents occurs within the testes in the walls of the tubuli contorti (Figs. 384 and 385), the origin of which must be sought in the embryo.

The embryonic genital ridge on either side between the mesonephros and the mesentery within the body cavity is composed of a mass of mesodermal cells that form the testis. The cells on the outside of this testicular mass facing the body cavity are arranged in a layer of epithelium which becomes invaded by the primordial germ cells.

By repeated mitoses of cells in this superficial layer, cordlike cellular masses push down into the undifferentiated cell mass of the testes. These solid cellular strands later become hollowed out and enormously elongated to form the different tubuli of the testes, in the walls of which are lodged the *spermatogonia*.

The ovary develops from the genital ridge in the female with a similar

outer stratification of epithelium in which are certain germplasmal cells that in mammals proceed to proliferate down into the substance of the ovary as cellular masses, called *Pflüger's cords* (Fig. 390). These cords, however, do not hollow out in the manner of the corresponding structures in the testes, but instead form *follicles*. Each follicle is characterized by the presence of a central primary cell, or *ovum*, surrounded by numerous follicular cells, which later may be sacrificed as nutriment for the cannibalistic egg cell within.

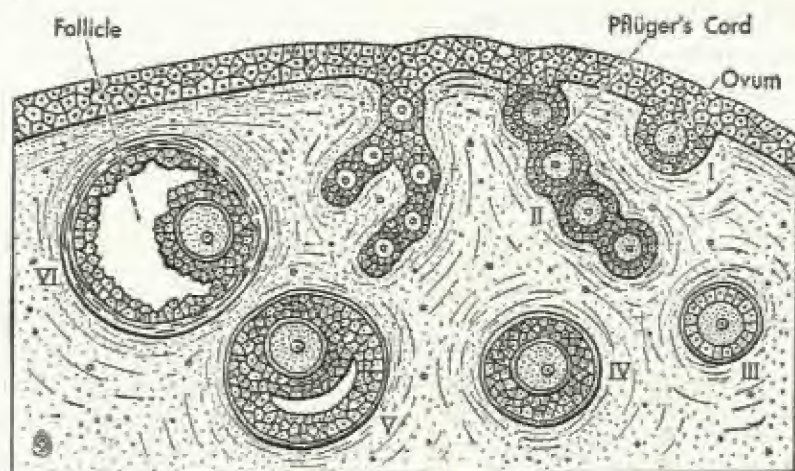


Fig. 390. Oögenesis. The genesis of the ovum, within the Graafian follicle in the ovary, is indicated by the successive numbers I-VI. (After Boule.)

In mammals the follicular mass, as *Graafian follicle*, becomes hollowed out and filled with fluid so that the developing ovum is practically surrounded by a double wall of follicular cells, like a lighthouse on a peninsula that projects into an inland sea.

The Graafian follicle migrates as a whole from its embedded position and gradually crowds to the surface of the ovary where it bulges out as the fluid-filled cavity increases in size. Eventually the wall of the follicle ruptures and the egg is extruded into the body cavity.

The cavity of the ruptured Graafian follicle immediately becomes filled with a blood clot, the *corpus haemorrhagicum*, which in turn is gradually invaded and replaced by peculiar yellow *lutein cells*, making the *corpus luteum*. This periodically recurring mass of cells has an important endocrine function, that will be referred to again in the following chapter.

Eventually the corpus luteum is obliterated by an invasion of connective tissue, leaving a scar on the surface of the ovary, the *corpus albicans*, which

is all that remains to tell the story of the origin of a mammalian egg. Successive phases of the development of the Graafian follicle in the mammalian ovary are shown in Figure 390.

2. Ducts

(a) **Disposal of Gametes.**—The body cavity may be regarded as an expanded gonadal sac, since the sex cells come to maturity on its inner wall and are shed into it.

There are at least three general ways among vertebrates by which the mature gametes finally escape to the outside, namely, (1) through pores in the body wall, no ducts being present; (2) through ducts continuous with the gonads; and (3) through ducts not continuous with the gonads and for the most part taken over from the mesonephridial apparatus.

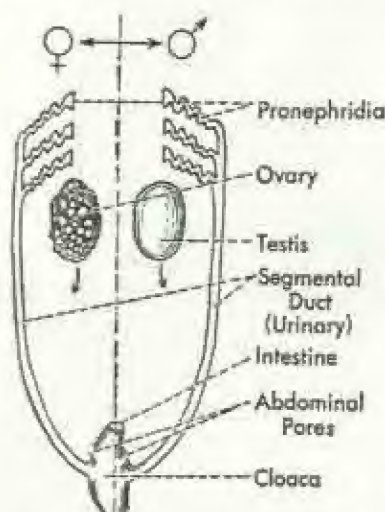


Fig. 391. Pronephridial stage of certain cyclostomes. Female represented on the left; male on the right.

abdominal pores is also utilized by a few teleost fishes belonging to the *Anguilliformes*, the various types of eels. Here, however, it is evidently a degenerate condition.

Many teleost fishes employ the second method of germ-cell disposal, that is, by means of direct ducts that are continuous with the gonads. The ova never enter the main body cavity but pass out directly through ducts united with ovarian sacs which entirely invest the gonads (Fig. 389). It will be recalled that the cavities of these sacs are pinched-off portions of the original main body cavity. Sperm cells are carried from the testis to the urogenital sinus by a genital duct which grows back from the testis completely independent of the mesonephros (Fig. 392).

The first of these avenues of escape is seen in amphioxus, whose gametes are extruded into the peribranchial chamber and thence out through the *atrial pore*. In some cyclostomes also, which receive eggs and sperm into the body cavity, *abdominal pores* furnish an exit through the posterior part of the body wall into the *urogenital sinus* behind the anus (Fig. 391). These pores are usually paired but may, as in *Petromyzon*, present a single opening through a projecting papilla. The method of disposal of sex cells through

The third method, that of indirect ducts, is by far the most common. In elasmobranchs, dipnoans, amphibians, reptiles, birds, and monotremes the ducts open into a *cloaca*, but in mammals other than monotremes, directly to the outside as a result of the longitudinal splitting of the cloacal region into a dorsal digestive portion and a ventral urogenital passage-way. Generally in this third group the sperm, never entering the body cavity at all, reach the sperm duct indirectly after passing through the long convoluted tubules of the epididymis, while the eggs always enter the body cavity from the ovary and are then picked up by the open ends of the unconnected oviducts for transference to the outside. There is, therefore, a fundamental difference in the disposal of the germ cells of the two sexes.

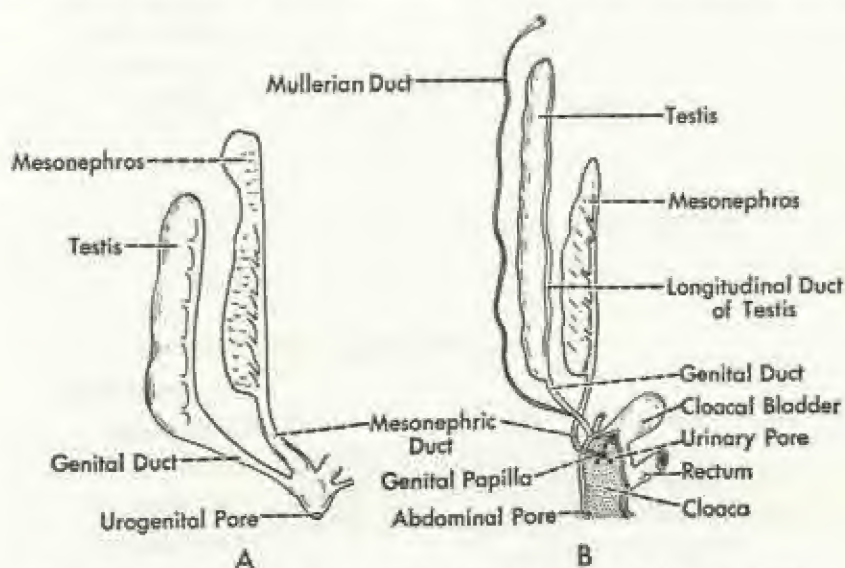


Fig. 392. Male urogenital organs in bony fishes, A, a teleost; B, *Protopterus*. (After Goodrich and Parker.)

(b) **Sperm Ducts.**—Exclusive of the teleosts there is an intimate relation, particularly in the male, between the ducts that dispose of the sexual products and the mesonephridial system. It will be remembered that the segmental ducts of the pronephroi (Fig. 391) remain after the pronephridia have been replaced by mesonephridia, to become the mesonephric, or *Wolfian ducts* (Fig. 393). These ducts not only drain the mesonephros, but in the case of male elasmobranchs and amphibians they also serve as sperm ducts, for which reason they are properly designated as *urogenital ducts*.

The connection of the urogenital duct with the testis is accomplished through the mesonephridia of the anterior part of the mesonephros, known

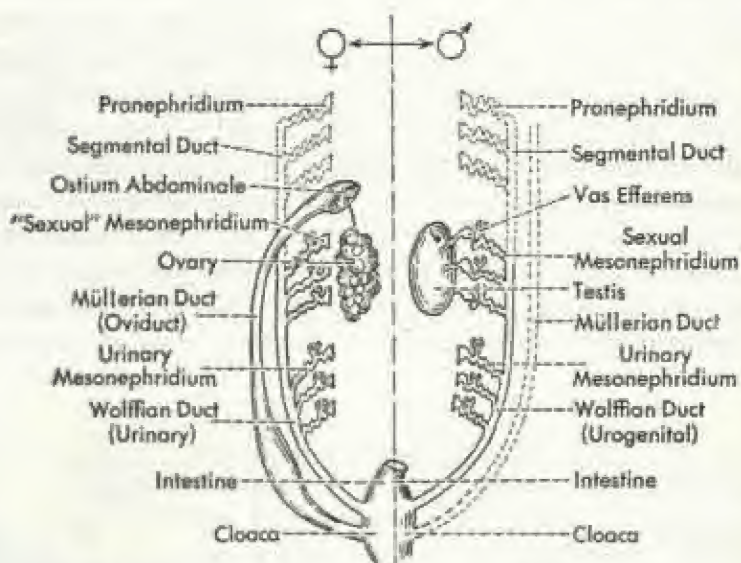


Fig. 393. Mesonephridial stage of fishes and amphibians.

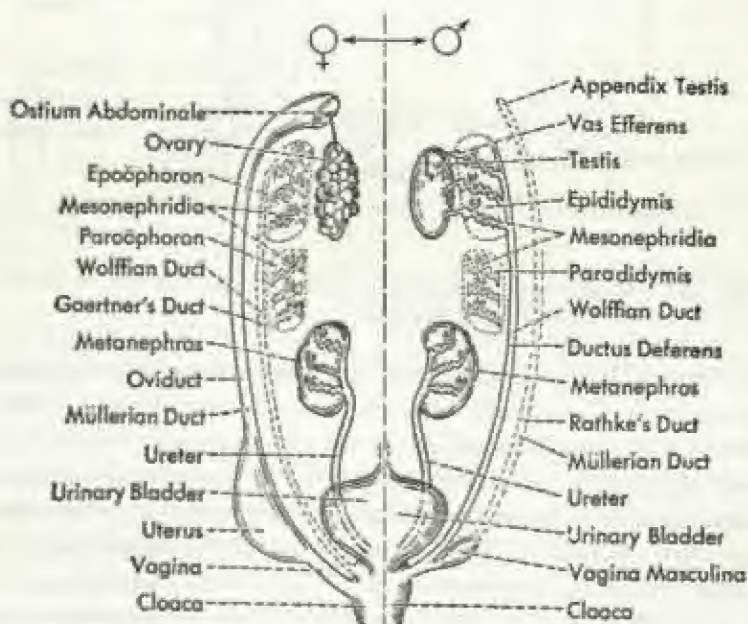


Fig. 394. Metanephridial stage of reptiles, birds, and mammals.

as the "sexual kidney," or *epididymis*, as distinguished from the posterior part, or "urinary kidney."

In male reptiles, birds, and mammals only the sexual kidney remains functional as the *epididymis*, while the urinary part of the mesonephros, being replaced by the permanent metanephric kidney, becomes degenerate (Fig. 394). The Wolffian ducts, however, persist as sperm ducts exclusively, in the guise of the *ducti deferentes*, or *vasa deferentia*, while the urinary products of the metanephros are disposed of through independently formed *ureters*.

After leaving the walls of the *tubuli contorti* in which they are originally embedded, the sperm cells pass through the *tubuli recti*, the *rete testis*, and *ductuli efferentes* to emerge into the *epididymis* (Fig. 384). This latter is essentially an organ made up of several *epididymal tubules*, or *cranial mesonephridia*, and a very much coiled part of the Wolffian duct, the *ductus epididymidis*. In reptiles the epididymidis is sometimes even larger than the testis itself.

The tubules in the epididymis are transformed mesonephridia which have lost their glomeruli and acquired a secondary connection with the rete testis through the so-called *junctional cords* of cells that later become hollowed out as the *ductuli efferentes*, making a continuous passage-way from the *tubuli contorti* in the testis to the outside.

In man the epididymal tubules, of which there are from nine to fifteen in each epididymis, are very much coiled and together form the *globus major*, or *caput*, of the epididymis. They still empty into the end of the Wolffian duct as they did before being converted from mesonephridia and transferred to the service of the reproductive system. The beginning of the Wolffian duct is also greatly convoluted and constitutes a mass known as the *globus minor*, or *cauda*, of the epididymis. From the *globus minor* the Wolffian duct emerges as the *ductus deferens*. The entire Wolffian duct in man, according to Lewis, is about twenty feet in length if straightened out. When the infinitesimal size of the human sperm cell is taken into consideration, its journey to the outside world from its point of origin in the testis is a comparatively extensive one.

Near the larger open end of the Wolffian duct there is usually a saccular expansion called the *seminal vesicle* (Fig. 384), which, although glandular in character, frequently serves the purpose of a temporary storage place for the traveling sperm, as its name would indicate.

In mammals there is a union of the urethra and the *ducti deferentes* beyond the points where the seminal vesicles open into them, so that the end of the sperm duct in an amniote, like the entire duct in the males of elasmobranchs,

branches and some amphibians, is *urogenital* in character, serving the double function of disposing of both sperm and urine.

That part of the ductus deferens between the seminal vesicle and the point of its junction with the urethra is termed the *ejaculatory duct* (Fig. 384). Its muscular walls by peristaltic action evacuate the sperm.

(c) **Oviducts.**—The oviducts are less directly related to the mesonephridial apparatus than are the sperm ducts. Early in embryonic life a second duct, the *Müllerian duct*, appears alongside the Wolffian duct (Fig. 393). This becomes the *oviduct*. It may form by longitudinal splitting of the segmental duct, as in elasmobranchs, or it may develop parallel to the segmental duct out of surrounding tissues either as a groove in the peritoneum that becomes closed off, or as a solid strand of cells that afterwards becomes hollowed out. Thus, the segmental duct may either split to form the Müllerian duct and the Wolffian duct, or persist undivided as the Wolffian duct.

Except in teleosts each oviduct opens freely into the main body cavity by an *ostium abdominale* (Figs. 393, 394, and 396). In some cases these open ends of the ducts may be located at a considerable distance from the ovaries themselves and the points where the eggs dehisce, or they may be close around the ovaries as in mankind, so that, while the eggs theoretically pass through the body cavity, there is little chance that they may escape therein and miss the openings into the ducts. Once within the oviducts the eggs are forwarded by peristalsis of the muscular walls.

The ostium abdominale in elasmobranchs is probably derived from a persistent mesonephridium that attained embryonic connection with the segmental duct (Fig. 375). Thus, the ostium abdominale, into which the ova from the body cavity are transferred, is homologous with the nephrostome of a nephridium that ancestrally served to drain the body cavity of fluids of excretion. There is no connection in other vertebrates, either in the male or in the female, between the embryonic Müllerian duct and the urinary apparatus.

In the exceptional teleosts there is an organic unity between ovary and oviduct, entirely preventing an excursion of the egg into the body cavity. In some carnivores, such as the walrus and seal, the ovary becomes so encapsuled within the lips of the ostium abdominale, that it superficially resembles the condition in teleosts.

Some elasmobranchs and marsupials have the open inner ends of the two oviducts fused together, forming a single ostium. Fusion at the cloacal ends of the two oviducts, however, is more common. It usually occurs in teleosts and certain Salientia as well as quite generally among the mammals.

In those animals that produce many eggs at one time, as the frog for example, the oviducts temporarily become enormously elongated and convoluted during the egg-laying season (Fig. 395). The oviduct of a pullet which has not begun to lay eggs is about six or seven inches in length, whereas in an egg-laying hen it is four times as long.

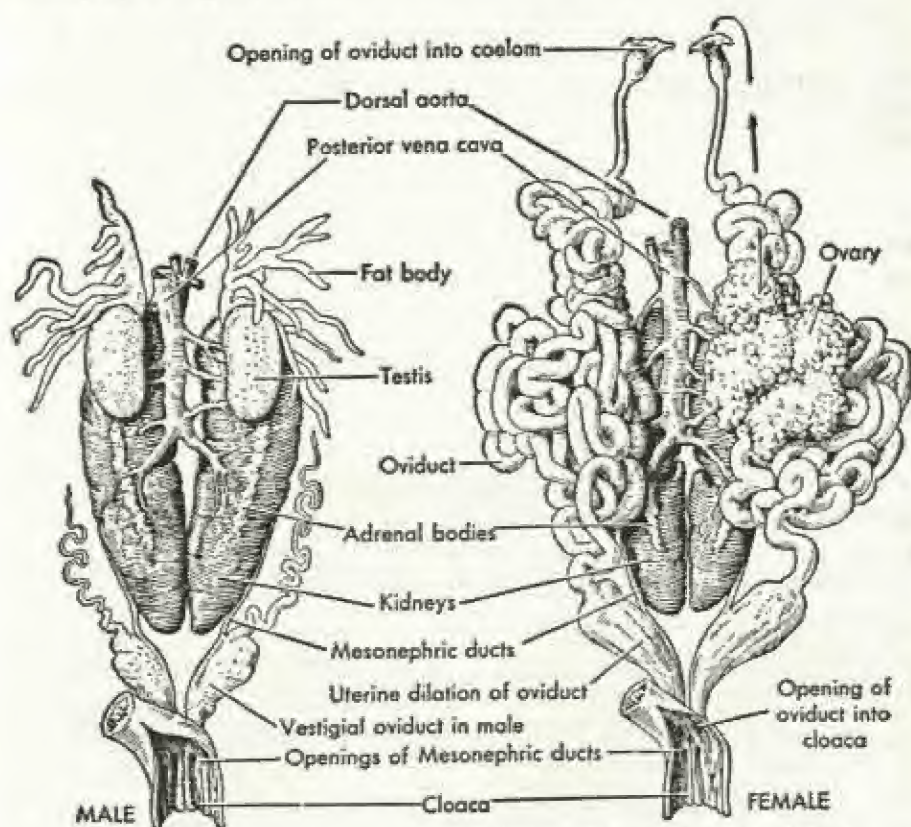


Fig. 395. The reproductive organs of the frog. (From Woodruff, *Animal Biology*, copyright 1941 by permission of The Macmillan Company, publishers.)

Among higher vertebrates the oviducts are made up of *Fallopian tubes* for the reception of the eggs from the ovaries, and nearer their exit they undergo extensive elaboration into *uterus* and *vagina*, modifications to be considered later.

Müllerian ducts are also present embryonically in the male, but in the adult they suffer various degrees of degeneration. The lungfish, *Neoceratodus*, and the newt, *Triton*, as well as the leopard frog, *Rana pipiens*, are exceptional cases, showing persistent Müllerian ducts in the adult males.

3. Apparatus for Effecting Fertilization

(a) **Fertilization of Animals and Plants Contrasted.**—Fertilization, or the union of egg and sperm, initiates the life history though not the life of a new individual.

Among plants the traveling male gamete, carried in the *pollen cell* on its way to the female gamete in the *ovule*, usually takes the air route, or steals a ride on some accommodating insect that acts the part of match-maker.

Such methods are not employed in the fertilization of the eggs of animals. The sperm cell in the case of all vertebrates goes forward in its search for the ovum by means of a vibratile tail that requires a fluid medium in which to travel.

Naturally, the problem is least complicated in the case of those vertebrates that find themselves in water when the germ cells are expelled from the body, since a suitable medium for the locomotion of the sperm is ready at hand. When, in the course of evolution, emergence onto land took place, the reproductive apparatus had to be greatly supplemented in order to bring egg and sperm together for the purpose of fertilization. It is evident that the sperm of non-aquatic animals must encounter the eggs while they are still in the body of the female, since sperm cells cannot locomote through the air. This necessitates the pairing of the sexes by actual contact, so that the sperm may be definitely placed within the oviduct, rather than by the promiscuous broadcasting of germ cells in the surrounding medium followed by chance union, as in aquatic vertebrates. Moreover, a fluid, indispensable for the lashing tails of the locomotor sperm cells, must be elaborated from special glands provided for the purpose in order that the distance within the oviducts between the entering sperm and the descending ovum may be successfully covered.

Whenever internal fertilization occurs, the egg is thereafter either provided with a protective shell and laid, to be subsequently incubated and hatched (*oviparous animals*), or it undergoes its preliminary development within the sheltering walls of the female body before venturing alive into the world (*viviparous animals*).

To insure the placement of the sperm within the oviduct, various holdfast mechanisms, as well as organs of copulation, have been evolved in different animals.

(b) **Holdfast Mechanisms.**—The amphibians, which are halfway land animals, have been so occupied with adapting themselves to a dual existence that apparently they have not been able to accomplish much in an evolu-

tionary way for their accessory reproductive apparatus. The result is that for the most part they return to the water during the breeding season, where fluid for the locomotion of the sperm cells is freely provided, and there is no necessity for elaborating organs to accomplish internal fertilization.

Amphibians do, however, improve upon the improvident and wasteful ways of most fishes, with their countless eggs and unthinkable numbers of sperm. For example, frogs practice *amplexation* during the breeding season (Fig. 28B), that is the male frog saddles himself on to the back of the female, whose body, unfettered by hooplike ribs, becomes more and more swollen by the increasing mass of eggs within. The male retains his grasp upon the slippery back of the female by means of temporarily roughened glandular swollen thumbs (Fig. 154), which are inserted under the armpits of the female and act as holdfasts. He remains in amplexation until the female extrudes the eggs, when he immediately sheds the sperm over them. In this way the hazards and uncertainties of distance between the germ cells of the two sexes are greatly lessened.

The hylas, or tree frogs, and the "obstetric frog" *Alytes*, of Europe, do not ordinarily resort to the water to breed, but Kammerer reports that when *Alytes* is compelled to breed in water, amplexation occurs and the thumbs of the male become swollen and roughened as in other frogs.

Many male lizards possess a row of peculiar porthole-like "glands" down the inner surface of the hind legs (Fig. 155). These femoral structures are not true glands, producing a liquid secretion. Instead they extrude a dry scaly substance that roughens the surface of the legs so that when the male lizard in mating grasps the female between his hind legs, the security of his grip is insured.

Snakes coil around each other in the mating embrace. The male boa-constrictor, according to Boas, is supplied with *anal hooks* that aid in holding together the cloacas of the two sexes during the transfer of sperm to the female.

Among higher vertebrates, organs already present but not especially evolved to accomplish the holdfast function in reproduction are utilized for this purpose. Thus, the cock when treading a hen employs his beak and claws. In animals like ruminants, where holdfast organs would be difficult to imagine, the sexual act is usually accomplished very quickly, as in the case of the tumultuous and almost instantaneous leap of the stag. Camels solve their copulation difficulties by assuming a sitting-down posture.

(c) **Male Copulatory Organs.**—Copulation consists of the introduction of a male copulatory organ, the *penis*, in which the sperm duct terminates, into the enlarged end of the oviduct, or *vagina*. The discharge of

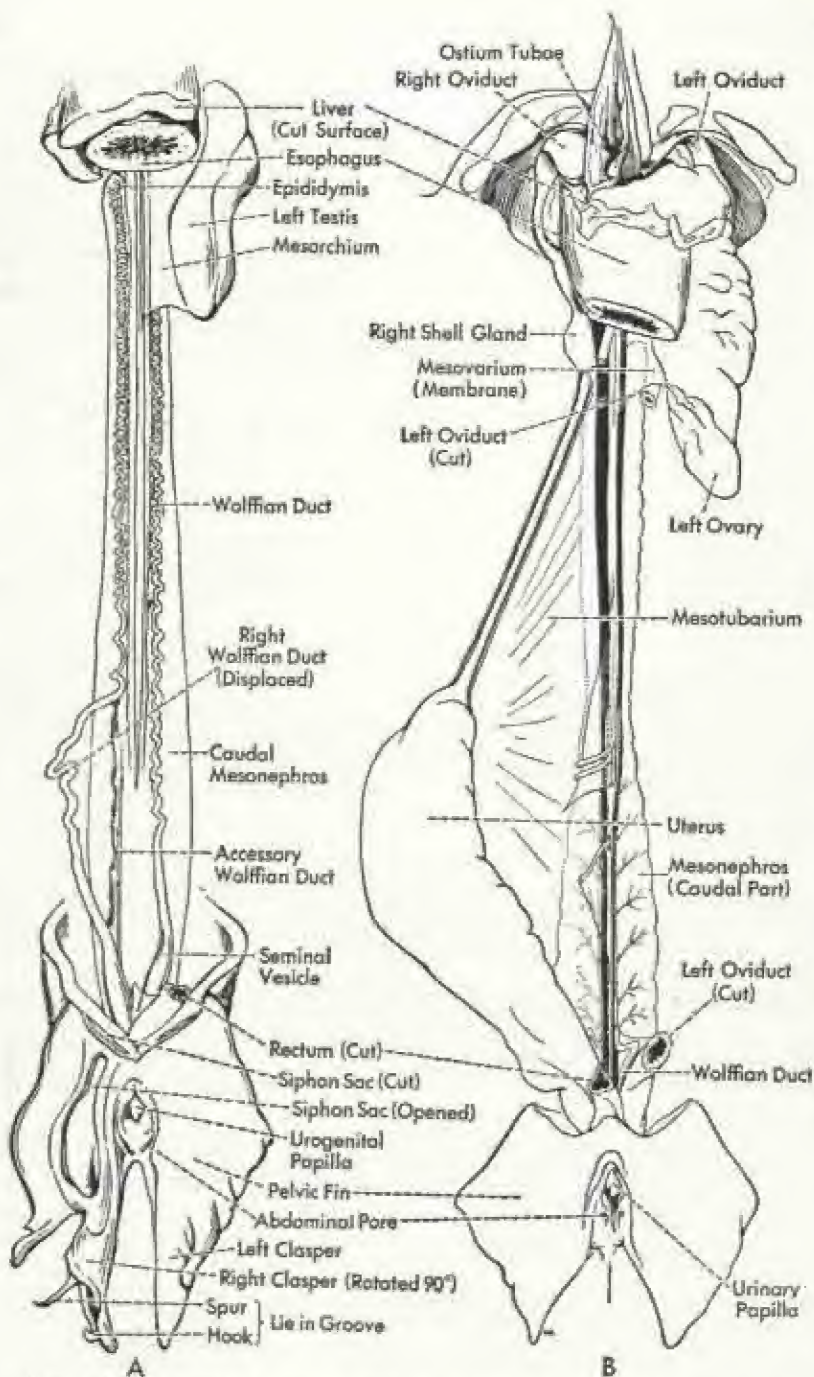


Fig. 396. Urogenital organs of the spiny dogfish, *Squalus acanthias*. A, male; B, female. In both cases the gonad of the right side was removed to show more dorsal structures. (From Sayles, *The Spiny Dogfish, Squalus acanthias*.)

the sperm cells under these circumstances makes more certain their placement in the immediate vicinity of the eggs to be fertilized.

It is to be expected that the apparatus for copulation in the aggressive male with sperm cells to deliver should be more elaborated than that of the receptive female, and such is the case.

Not all the organs for copulation among vertebrates are homologous. Thus, male elasmobranchs of many species possess a pair of "claspers," one on each side of the cloaca, which are modifications of the medial parts of the pelvic fins (Fig. 396). In these animals, whose young are "born alive" in an advanced stage of development, copulation and internal fertilization are effected by the aid of these claspers, equipped with hooks, which are inserted into the cloaca of the female and serve to direct the sperm along their grooved inner margins into the oviducts (Fig. 397).



Fig. 397. Dogfish in copulation. (After Bolau.)

Rarely a similar contrivance is found among teleosts, that serves as an intromittent organ. This is formed sometimes out of the ventral or anal fin, as in the strange Brazilian bony fish, *Girardinus*, and sometimes from the metamorphosed haemal spine of a caudal vertebra.

It is with land life, however, that the evolution of internal fertilization and attendant copulatory mechanisms really begins, although none of the amphibians have a penis, with the possible exception of the footless caecilians. In these tropic amphibians, which have taken to land life in damp situations, the walls of the male cloaca during copulation are everted into the cloaca of the female, thus serving as an intromittent device.

Internal fertilization without the assistance of copulatory organs is accomplished among certain urodeles, *Triturus*, *Amblystoma*, *Triton*, and the viviparous *Salamandra atra* of Alpine streams, by a very different method. The males during the breeding season deposit their sperm in small compact packets or *spermatophores*, surrounded by a protective gelatinous mass, while the females follow after the males as the spermatophores are produced, and use their cloacal lips to pick up the spermatophores, even when the latter are deposited on land as sometimes occurs.

Among modern reptiles two types of penes have been evolved. First, among lizards and snakes, *double cloacal organs* are found, which may be everted somewhat after the manner employed by caecilians. Each *hemipenis* has a spiral groove along its medial surface for the conveyance of the sperm. Second, turtles (Fig. 398A) and crocodiles have a single penis, lying

along the ventral wall of the cloaca, slightly protrusible and supplied with erectile tissue, dorsally grooved along its length. During copulation this groove is made into a temporary canal by its contact with the upper dorsal wall of the cloaca.

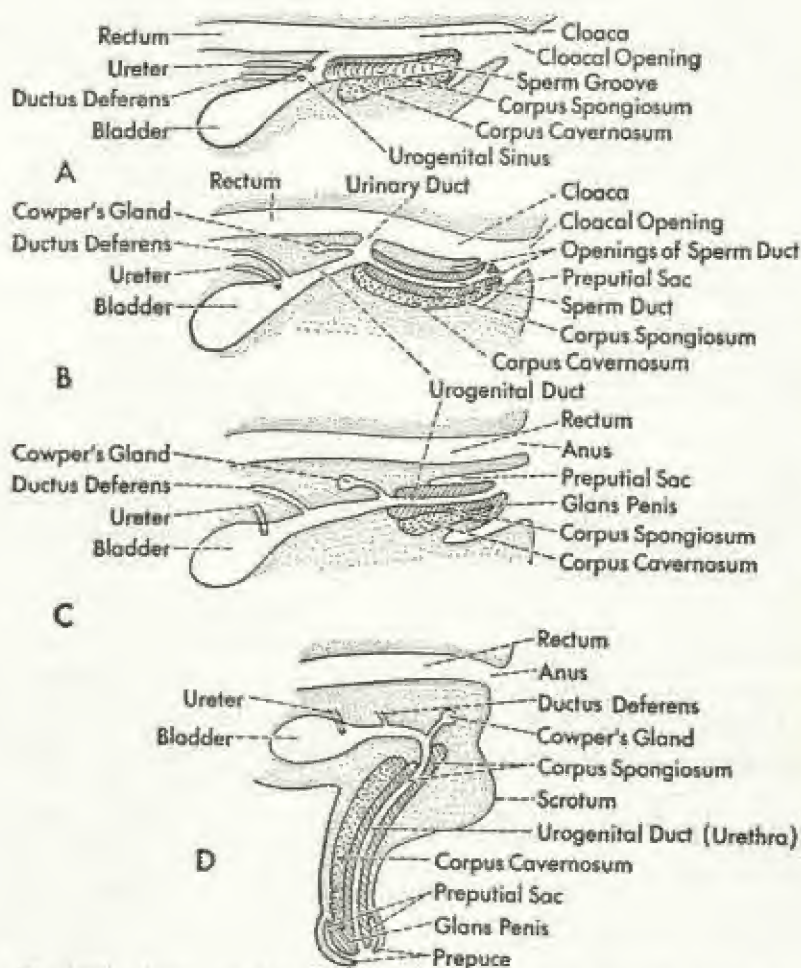


Fig. 398. Stages in the evolution of the penis. A, tortoise; B, spiny anteater; C, kangaroo; D, man. (After v.d. Broek; Boas.)

The single penis of the crocodiles is formed by two component parts suggesting a double origin. In turtles the size of the penis bears a distinct relation to the difficulties encountered in copulation because of the awkward shell. It is smaller in marine turtles having a flattened or incomplete plastron, than in fresh-water or land forms with a more complete and over-arching shell.

Among birds there is no true copulation, but impregnation by the method of the cloacal kiss is the general rule. There are, however, a few birds, notably ostriches and other ratitates, certain ducks, and the South American "tinamou," which have well-developed penes, resembling those of crocodiles.

The penis in all mammals, with the exception of monotremes (Fig. 398a), is a closed tube and not a grooved structure as in reptiles. Intermediate forms between reptiles and mammals are not known. It is typically a turgescient organ under the control of vaso-dilator nerves

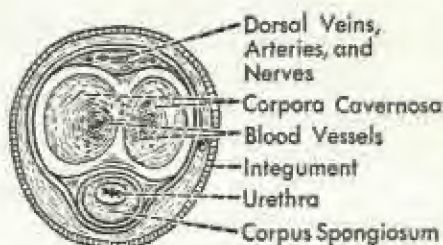


Fig. 399. Transverse section through middle of human penis. (After Toldt.)

which arise as autonomic fibers in the sacral region of the spinal cord, and is composed of two masses of erectile tissue side by side, the *corpora cavernosa*, with a third similar mass, the *corpus spongiosum* beneath them, held together by fibrous tissue and enveloped by a layer of loose skin (Fig. 399).

The corpus spongiosum is perforated for its entire length by the urethra. Consequently the urethra is considerably longer in the male than in the corresponding female. It terminates in an enlargement of the corpus spongiosum called the *glans* (Fig. 398b), which is split in marsupials where the female has a double vagina.

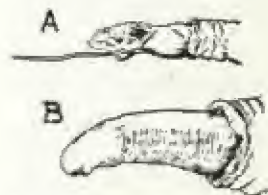


Fig. 400. A, distal end of ram's penis, showing glans and *processus urethralis*, or filiform appendage. B, distal end of bull's penis, showing glans and urethral papilla, representing vestigial filiform appendage. In both cases the prepuce is folded back. (After Marshall.)

In some animals, for example the cat, guinea pig, and wombat, the glans is beset with horny recurrent spines or corneal scales that stimulate the female during copulation, although in most cases the skin extending over the surface of the glans is extremely sensitive and delicate without any hard corneal layer. Ruminants, cetaceans, and some rodents are exceptional in that there is no glans present, while sheep, goats and many

antelopes possess a peculiar threadlike elongation of the sperm duct beyond the end of the penis itself, called the *processus urethralis* (Fig. 400).

Among higher animals the glans is enveloped in a double fold of retractile skin, the *prepuce* (Figs. 384 and 398b). This is present only in forms with a pendent penis and is homologous with the sheath in which the penis is withdrawn in many animals such as ungulates.

In several kinds of mammals, namely, marsupials, cetaceans, moles, carnivores, rodents, bats, seals, lemurs, monkeys, and some apes, there is present in various degrees of development, lying in the connective tissue between the two corpora cavernosa and above the urethra, a penis bone, *os priapi*, which increases the rigidity of the organ which in most cases is attained by temporary turgidity caused by an influx of blood.

Among mammals the obliteration of the cloaca goes hand in hand with the evolution of the penis, or *phallus* (Fig. 398). In monotremes a cloaca is still present, and the small non-protrusible penis is enclosed in a sac between the urogenital sinus and the cloaca itself. It is a fibrous, slightly erectile structure of double origin, with a groove between the two parts that is converted into a canal except posteriorly where the urogenital and cloacal passages still connect with each other. The ureters, instead of terminating in the bladder with a urethral outlet for the urine, empty through a urogenital sinus into the cloaca, the penis being utilized solely for the conduction of the sperm.

The marsupial penis, with the reduction of the cloaca, becomes an external erectile structure directed backward, through which both urine and sperm have common passage-way, as in all higher mammals. The *scrotum* containing the testes is located anterior to the penis. The distance between the penis and the anus is so slight in these animals that both penis and anus are enclosed together within a common muscular sphincter. The opossum *Didelphys*, the bandicoot *Perameles*, and some other species, have a bifurcate glans that is probably correlated with the double vagina in the females of these forms.

Among placental mammals the penis is in front of the scrotal sac and usually withdrawn within a protective sheath, except during sexual activity. In most cases it is directed forward and, when no sheath is present, is pendulous, as in bats and man. In monkeys and apes it is partly pendulous and partly ensheathed. In cats and rodents it is directed backward, except during copulation, so that these animals micturate posteriorly. Armadillos, handicapped by their awkward armor, have a relatively enormous penis which may extend as much as one third of the length of the body during copulation.

(d) **Female Genitalia.**—The female genitalia concerned in copulation, aside from certain glands and the rudimentary *clitoris*, are the vagina, vestibule, hymen, and the labia minora and majora (Fig. 401). All of these structures are differentiated to a point comparable with the degree of evolution attained by the copulatory organs of the corresponding males, reaching their maximum in the primates.

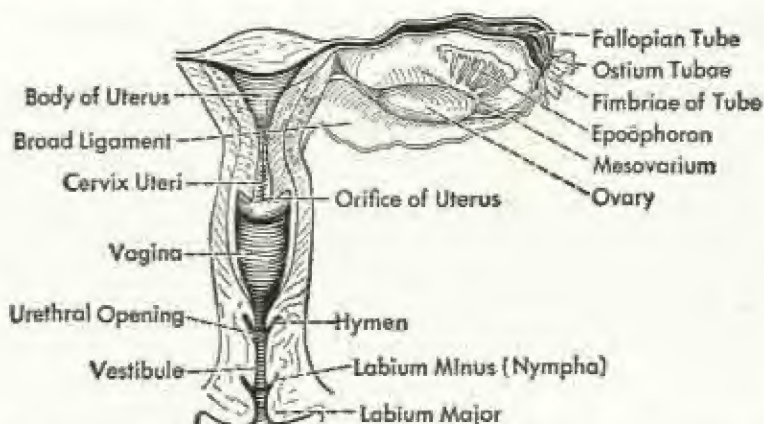


Fig. 401. Dorsal view diagram of human female reproductive organs. (After Toldt.)

The *vagina* is that part of the oviduct adapted to receive the penis. It is absent in the monotremes where the cloaca serves the same purpose. In the opossum, *Didelphys*, and other marsupials, there are two distinct vaginas which barely coalesce into one at the outer entrance, while in some other marsupials there is a coalescence at the inner ends from which a median diverticulum, or third vagina, extends posteriorly as a blind alley between the two lateral vaginas (Fig. 402). Whenever a fetus becomes deposited in this closed middle vagina instead of in one of the two lateral open passage-ways, there must be a rupture at birth at the blind end of the middle vagina to allow for the expulsion of the young.

In placental mammals the outer ends of the two oviducts open into a single vagina, located between the rectum dorsally and the urethra ventrally (Fig. 367). It is lined with mucous membrane, frequently crossed by transverse rugae, particularly in young individuals. The vaginal mucosa is without glands, the mucus that is present there coming from the walls of the uterus, especially the cervix, which is continuous with

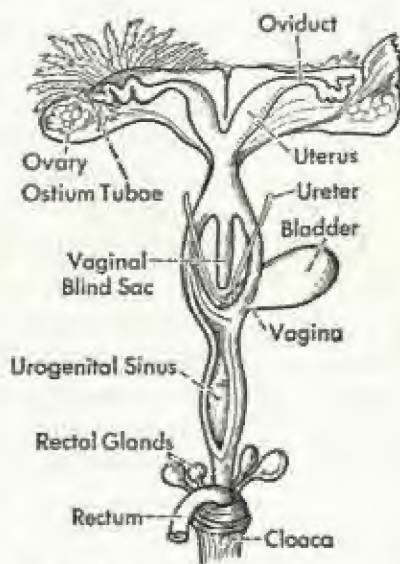


Fig. 402. Female urogenital organs of the wombat, *Phascogomys*, a marsupial. (After Wiedersheim.)

the vagina. The walls of the vagina are muscular and collapsible, and the muscular fibers near the external orifice form a sphincter.

The outer part of the vagina constitutes the *vestibule*, which is separated from the vagina proper by a temporary fold of mucous membrane, more or less complete, called the *hymen*. This is the real end of the embryonic Müllerian duct, and it partially occludes the passage-way, particularly before copulation has taken place. Originally in all mammals, the hymen persists in bears, seals, hyaenas, and most apes, but is present only in the young of the horse, pig and mole.

The walls of the vestibule are supplied with erectile tissue which at times becomes surcharged with blood. In primates generally around the vestibule on either side are two folds of skin, the *labia minora*, while in the higher primates there are in addition two external folds, the *labia majora*, covered outwardly with pubic hair and supplied with a certain amount of fatty tissue. There is also a pad of adipose tissue anterior to the vestibular orifice at the edge of the pubic bones. Likewise covered with hair, it is called the *mons Veneris*. It is better developed in the human females of civilized races than in those of more primitive types. The female bushman is remarkable for the hypertrophy of the labia minora, as well as for the enlarged posterior gluteal muscles, resulting in enormously prominent buttocks, or the condition described as *steatopygy* (Fig. 403).



Fig. 403. Female Australoid bushman, showing steatopygy. (After Martin and Schulze.)

The *clitoris* in the female is homologous with the penis in the male. It is situated just anterior to the vestibular opening between the folds of the labia minora and consists of two corpora cavernosa that are erectile, but there is no corpus spongiosum present, and the clitoris is not traversed by the urethra like the male penis, except in a few rodents, insectivores, and lemurs. In this latter case the urethra is not a urogenital canal, as in the penis, but is exclusively for the transmission of urine, as in other mammals. An imperforate clitoris is present in turtles, crocodiles, and a few exceptional birds whose males possess a penis. There is even a clitoris bone in certain mammalian species that corresponds to the os priapi of the male. The clitoris, which is relatively large in monkeys, being six or seven centimeters long in the young spider monkey, *Ateles*, is comparatively small and degenerate in the human female.

4. Accessory Glands

Associated with the reproductive apparatus are various glands which (1) provide a fluid medium for the locomotion of the sperm cells; (2)

facilitate copulation by reducing friction; (3) produce odors that are alluring to the opposite sex; and (4) furnish nutriment for the developing young. These glands may be grouped according to their place of origin into those (1) in the sperm duct or oviduct; (2) in the urogenital canal; or (3) in the integument.

(a) **Originating in the Sperm Duct or Oviduct.**—In many cases, for example in ruminants, most rodents, dogs, bears, martens, and shrews, the outer end of the sperm duct, near its entrance into the urethra, enlarges into an *ampulla*, which serves as a temporary reservoir for the sperm. This is lined with *ampullar glands* that secrete mucus. Such glands are absent in the cat, mole, European hedgehog *Erinaceus*, and the pig. In most mammals a saclike *seminal vesicle* (Figs. 384 and 404), lined with mucous glands, empties into each ductus deferens just beyond the ampulla. Between the seminal vesicle and the urethra the sperm duct is known as the ejaculatory duct. In general these vesicles have a glandular rather than a storage function, although sperm cells are frequently found therein. In the case of bats and some mice, the seminal vesicles enable these animals to exercise a sort of "birth control," in that after copulation the mucus that they produce forms a gummy plug which fills the entrance to the uterus, the cervical orifice, and prevents for a considerable time subsequent impregnation. There are no seminal vesicles in monotremes, marsupials, cetaceans, or carnivores. In man they appear first about the end of the third month of fetal life.

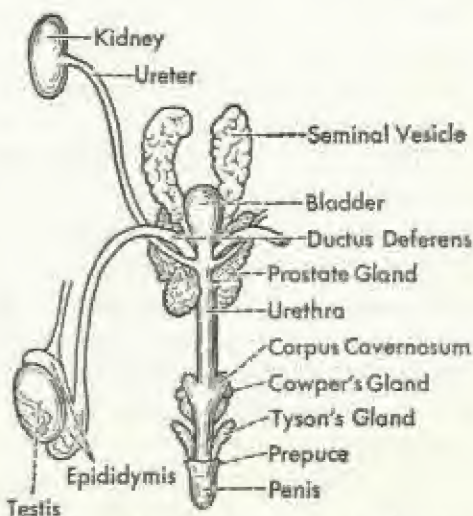


Fig. 404. Urogenital apparatus of a hamster, *Cricetus*. (After Gegenbaur.)

In the human female there are present at least three sorts of glands, namely, uterine, cervical, and vestibular, associated with corresponding regions of the oviduct.

The *uterine glands* are tubular structures lining the uterus. They have to do with the epithelial regeneration of the uterine walls during menstruation, rather than with glandular secretion.

The much branched *cervical glands*, found in the cervix of the uterus, produce mucus which moistens the inner surface of the glandless vagina,

while the scattered *vestibular glands*, located in the vestibule near the clitoris and around the outlet of the urethra, perform a similar function.

(b) **Originating from the Urogenital Canal.**—The glands of the urogenital canal are the prostate, in the male, and the urethral glands, which appear in both sexes.

The *prostate gland* (Fig. 384), in man at least, is the most important of all the accessory reproductive glands. It is a compound tubulo-alveolar gland about the size of a horse-chestnut, made up of thirty to fifty lobules and opening into the urethra by means of two large and fifteen to thirty lesser ducts. It is embedded in a tough capsule of connective tissue and abundantly supplied with blood, nerves, lymph, and more smooth muscle cells than any other accessory reproductive gland. It surrounds the beginning of the urethra at the point where the ducti deferentes, or sperm ducts, enter.

The secretion produced by the prostate gland, forming a large part of the *semen*, or spermatic fluid, is a thin milky emulsion, faintly alkaline with a characteristic odor. The prostate gland is well developed in rodents, bats, perissodactyls, primates, and most carnivores. It is less well developed in ruminants, and is absent in monotremes, marsupials, edentates, and among carnivores, in the marten, otter, and badger. In man the prostate gland frequently becomes hypertrophied in old age and may deposit concretions of calcium phosphate, causing trouble by pressure upon the urethra which it envelops.

The urethral glands are of two sorts. First, mucous glands, called *glands of Littre*, in the male, that are most numerous in the dorsal region of the urethral wall along the penile part of its course; and second, paired *bulbo-urethral glands*, called *Cowper's glands* in the male and *Bartholin's glands* in the female.

Cowper's glands are two small structures about the size of peas in the human male, with ducts an inch long opening into the urethra at the base of the penis. They produce a clear glairy mucus during sexual excitement which protects the sperm against traces of acid that may be present. Bears, dogs, and aquatic mammals lack Cowper's glands, but in other mammals they are quite generally present, being especially large and active in rodents, elephants, pigs, camels, and horses. They are the only accessory reproductive glands in the male *Echidna*.

Corresponding to Cowper's glands of the male, are the glands of Bartholin in the female, that open into the vestibule in the groove on either side between the hymen and the labia minora. They produce mucus which functions largely as a lubricant during copulation.

In the formation of the semen it has been shown that the first contributions come from Cowper's glands and the glands of Littre, followed by the secretion of the prostate gland before the sperm from the ductus deferens are added, while the final glandular contribution is from the seminal vesicles.

(c) **Originating in the Integument.**—Various odoriferous glands of integumentary origin, named in different cases *anal*, *inguinal*, *perinaeal*, and *cloacal glands*, occur among vertebrates. These are usually located around the anus or genital aperture and serve to stimulate the opposite sex. The famous scent glands of skunks belong to this category, as do also the anal glands of dogs, which are well known to be of paramount importance in the social life of these animals.

Tyson's glands are small sebaceous glands that are situated around the base of the glans on the penis in the depths of the preputial fold of skin. They also produce an odorous substance called *smegma*.

The male alligator has *submaxillary glands* at the edge of the lower jaw on either side, which enlarge and emit a musky odor during sexual excitement.

Finally, under integumentary glands there should be mentioned the *mammary glands*, already described in a previous chapter, that have a place in the general scheme of reproduction in the mammals, since they provide sustenance for the newly born young. Marsupials, which have no true placenta, nourish the fetus before birth with "uterine milk" produced by uterine glands.

5. Devices for the Care of Eggs and Young

(a) **Uterus.**—With most animals that practice internal fertilization, a part of the oviduct becomes modified into a brood organ, the *uterus*, for the protection of the developing embryo. This structure is located midway between the upper portion of the oviduct, called in human anatomy the *Fallopian tube*, which receives the egg from the ovary, and the vagina below. The virgin uterus is completely within the pelvis but during pregnancy it is shifted to a position higher up in the abdomen. Its thick muscular walls are capable of great distension, enlarging over 200 times when accommodating a growing fetus. When unoccupied by young the cavity within the uterus is relatively small and the shrunken inner walls are more or less in contact with each other. The rounded mouth of the uterine cervix, where it meets the vagina, frequently projects somewhat into the vaginal cavity (Fig. 401).

Even in frogs the oviduct during the breeding season enlarges at its

cloacal end into a "uterus" for the temporary lodgment of the eggs. Viviparous teleosts, as also some elasmobranchs, have a well-developed highly vascularized uterus. Mammals, however, show the greatest differentiation of this organ.

A uterine modification of the oviduct, when found among lower vertebrates, is usually a double structure, one for each oviduct, but with increasing coalescence of the oviducts in mammals to form a single vagina, there is a tendency for this fusion to involve either a part or the entire uterine region. All the theoretical intermediary evolutionary stages from a double uterus to a single one have their actual counterparts in nature among mammals.

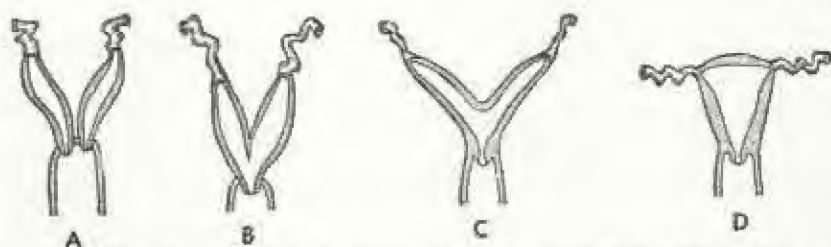


Fig. 405. Types of uteri. A, uterus duplex; B, uterus bipartitus; C, uterus bicornis; D, uterus simplex.

Thus, there are two distinct uteri (*uterus duplex*, Fig. 405A) without vaginas in monotremes, and each with a separate vagina in marsupials. Among placental mammals, some rodents, for example the mouse, hare, marmot, and beaver, as well as elephants, certain bats, and the "aard-vark" *Orycteropus* of South Africa, have a duplex uterus which opens into a single vagina. A beginning of coalescence between the two uteri (*uterus bipartitus*, Fig. 405B) is apparent in pigs, cattle, certain rodents, some bats, and carnivores. A two-horned uterus (*uterus bicornis*, Fig. 405C) is characteristic of ungulates, cetaceans, insectivores, and some carnivores, while a single uterus (*uterus simplex*, Fig. 405D), with two slender Fallopian tubes projecting from it, is the type found in apes and man.

Various pathological anomalies that suggest doubling are encountered in the human uterus, which find a ready explanation in the story of the comparative anatomy of this organ.

The curious South American teleost *Girardinus*, already mentioned as having a metamorphosed haemal spine of a caudal vertebra for a copulatory organ, has a hollow ovary that serves as a uterus or brood sac for the young. The eggs, which debisce into the cavity of the ovary after the teleostean tradition, are fertilized in place by sperm that penetrate all the way

into the ovarian cavity, where the early stages of embryonic development occur.

(b) **Brood Sacs.**—Among vertebrates there are various instances, more or less exceptional, of brood sacs for eggs or young, aside from the uterus of the female. For example, among fishes there is a modification of the pelvic fins into a brood sac on the ventral side of the male pipefish, *Syngnathus*, into which the eggs are deposited by the female. In the sea-horse, *Hippocampus*, a relative of the pipefish, there is a similar arrangement whereby the male becomes responsible for the care of the eggs (Fig. 18A).

Among amphibians a dorsal pouch is located on the back of the female frog, *Nototrema pygmaeum*, of Venezuela, for carrying eggs (Fig. 28F), while the male *Rhinoderma darwini* of Java contributes his vocal sacs temporarily to serve as brood pouches (Fig. 28H).

The transient brood sac of monotremes and the permanent "marsupium" of the marsupials among mammals are further examples of structures belonging to the reproductive apparatus, since they obviously have been developed in the interests of the race rather than of the individual.

(c) **Nidamental Glands.**—Eggs destined to leave the body of the female before development are provided with some sort of a protective envelope or capsule. In water this does not need to be a very complicated structure, but exposure to dry air demands a shell of some kind.

It is apparent that fertilization must occur before the shell is put on to the egg, otherwise the sperm would encounter an insuperable barrier. Consequently *nidamental glands*, which produce the shell, are located in the walls of the oviduct some distance from the *ostium abdominale*, in order to allow opportunity for the egg and sperm to meet before the shell is added. Incidentally, putting a workman-like shell around a soft egg is an accomplishment which would be baffling to a human inventor.

Albumen glands, that furnish the "white of the egg," are also located in the walls of the oviduct between the *ostium abdominale* and the *nidamental glands*, since this extra store of nutriment must be added after fertilization, but before the egg is encased in a calcareous shell. The familiar cackling of a hen that has just succeeded in laying an egg is a true song of triumph, stimulating to a comparative anatomist who appreciates something of the intricacies of its elaboration.

Not only does the calcareous shell protect the exposed egg from injury, but, in the case of many birds, blending colors or blotches which help to camouflage it from searching enemies are deposited in the substance of the shell.

The aquatic eggs of the internally fertilized elasmobranchs are enclosed

in purselike horny capsules, supplied at each corner with curling tendrils (Fig. 381), which entangle them among seaweeds, so that the embryo fishes sway and rock within their curious cradles in comparative security until ready to emerge.

(d) **Placenta in Mammals.**—True mammals provide a placenta for the developing young. This is an elaborate compound vascular organ, made up

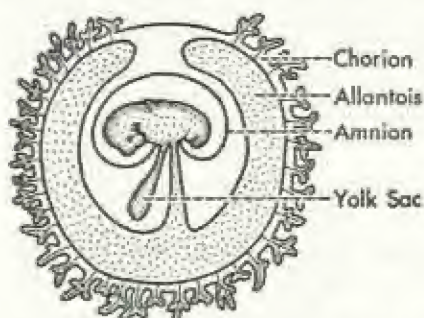


Fig. 406. Diagram of the embryonic envelopes of a mammal.

of interdigitating villi from the walls of the uterus and from the allantois of the embryo (Fig. 406), which brings the capillaries of the mother into intimate contact with the capillaries of the fetus, thus establishing a nutritive and respiratory bridge between mother and offspring.

There are other embryonic devices in mammals, such as the amnion and other fetal envelopes, which provide for the welfare of young reptiles,

birds, and mammals. These should not be overlooked in reckoning up the anatomical contrivances that aid in the preservation of the species.

6. Degenerate and Rudimentary Organs

With the supplanting of the pronephros and mesonephros by the metanephros among amniote vertebrates, there are left behind several structures in the developing animal that are deprived of their original usefulness. Some of these structures, like the mesonephric tubules which become transformed into the epididymal tubules of the male, are rescued and made over to serve a new function. Many other structures, however, degenerate, finding their way to the anatomical rubbish pile where they remain as useless parts of the animal mechanism, even becoming a source of pathological ills.

There are various *rudimentary organs* also that are useless because they never attain functional efficiency. Unlike degenerate structures which have had their day, these are incipient organs that have never completely developed.

It is quite important for the pathologist to be thoroughly grounded in comparative anatomy, since it is just these degenerate anatomical relics and rudimentary structures that are most likely to prove the focal points for the formation of cysts, tumors, and other bodily abnormalities.

The young embryo presents a condition with respect to the reproductive apparatus, for example, that suggests a hermaphrodite with the rudiments

of both sexes present. As development proceeds one sex becomes dominant, and the structures which characterize the other sex fade into the background as degenerate or rudimentary remains. There results a homology or equivalence in the anatomical details of the two sexes which is summarized in the case of man in Table VI, adapted from Wiedersheim.

TABLE VI. Table of Homologies of Structures Derived from the Mesonephros and Its Associated Ducts

		MALE	FEMALE
Mesonephros	Sexual part	Appendix epididymidis <i>Epididymis</i> (in part) <i>Rete testis</i>	Epoöphoron (in part.)
	Urinary part	Paradidymis Ductuli aberrantes	Paroöphoron
Wolffian duct	Proximal part	<i>Epididymis</i> (in part) <i>Ductus epididymidis</i>	Epoöphoron (in part)
	Distal part	<i>Ductus deferens</i>	Gaertner's duct
Müllerian duct	Proximal part	Appendix testis	<i>Fallopian tube</i> <i>Uterus</i>
	Distal part	Vagina masculina Colliculus seminalis	<i>Vagina</i> <i>Hymen</i>

The organs in this table that are in italics are functional, while the others are either degenerate useless structures or of doubtful function.

The *epoöphoron* of the human female is an organ lying between the layers of the *broad ligament* of the uterus, composed of eighteen or twenty anastomosing mesonephridia that are closed at both ends (Fig. 407). In ruminants, perissodactyls, and pigs, the mesonephridia forming the *epoöphoron* are connected with a fragment of *Gaertner's duct*, which corresponds to the Wolffian duct in the male.

The *paradidymis* and the *paroöphoron* in the two sexes respectively are all that remain of the posterior mesonephridia. The *paradidymis* lies within the spermatic cord near the *globus major* of the epididymis. Both the *paradidymis* and its homologue in the female are found only in older embryos and young children.

The *ductuli aberrantes* are also tubules, originally nephridia, blind at one end and opening into the duct of the epididymis. There may be one,

two, or several of them, although the number is usually two. They lie between the testis and the epididymis. The "inferior ductule," which is the more constant of the two, may attain the length of two inches in man.

The *appendix epididymidis* (Figs. 384 and 407), which is a degenerate tip of the mesonephros, lies upon the globus major of the epididymis. Toldt found it persisting in 29 out of 105 human autopsies. A similar structure is sometimes found in the female.

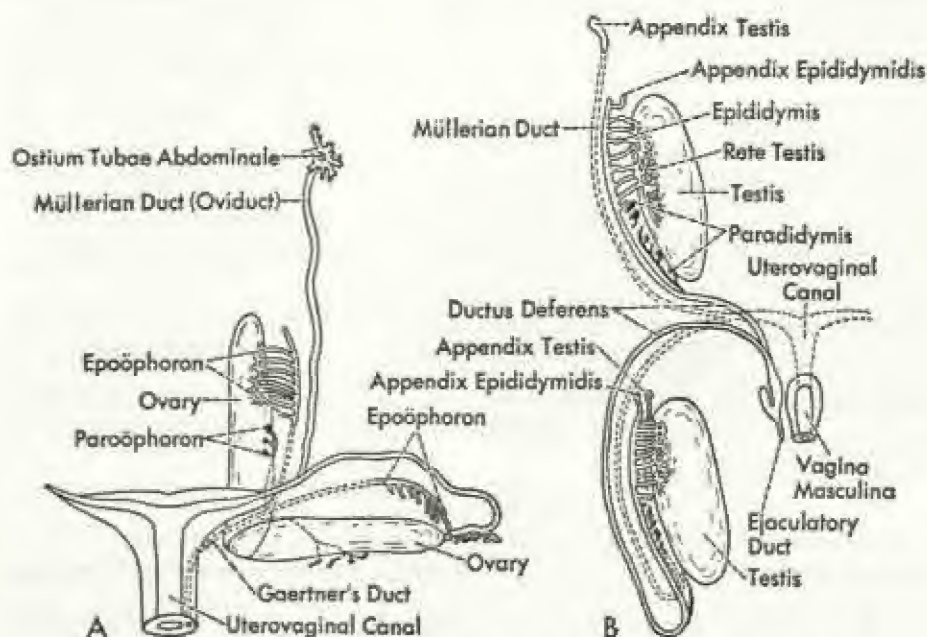


Fig. 407. The urogenital organs of man before and after descent. A, female; B, male. (After Felix in Keibel and Mall.)

The *appendix testis*, a small spherical sac attached to the testis (Figs. 384 and 407), represents the tip of the Müllerian duct. It has been reported as present in 90 per cent of the cases examined.

The other end of the embryonic Müllerian duct remains in the male in the form of the *vagina masculina*, a small sac homologous with the vagina. It is embedded in the prostate gland along with the base of the urethra and is usually distally bifid (Figs. 384 and 407), which is additional evidence that it represents the remains of coalescing oviducts.

Around the opening of the vagina masculina is a small fold of tissue, the *colliculus seminalis*, that marks the ends of the Müllerian ducts, and is homologous with the hymen of the female, which partially separates the

vagina from the vestibule, and likewise locates the true termination of the Müllerian ducts.

V. DETERMINATION AND DIFFERENTIATION OF SEX

The *determination of sex*, as pointed out in Chapter VI, probably occurs at the time when the egg is fertilized, depending on the chance combination of the sex chromosomes. The *differentiation of sex*, on the other hand, or

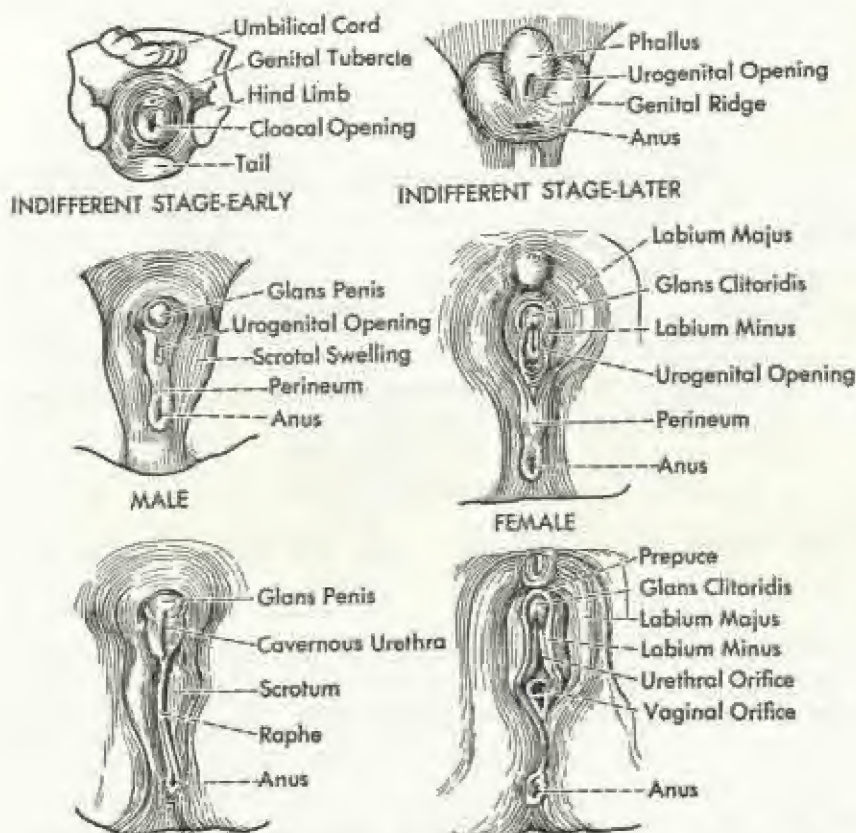


Fig. 408. Embryonic differentiation of external genitalia. (After Gray.)

the development of visible distinct sex characters, does not occur in man until about the ninth week of fetal life, although, according to Keith, the testes within the body cavity are distinguishable from the ovaries by the seventh week.

The human external genitalia of the two sexes at first cannot be told

apart. At the stage of about the sixth or seventh week, when the legs are simply two stubs on the two sides of the cloaca (Fig. 408), an elevation, the *genital eminence*, tipped by a conical projection, the *genital tubercle*, appears just within the anterior margin of the cloacal opening. Around the genital opening there forms a pair of folds, the *labio-scrotal folds*, which are destined to become either the labia majora of the female or the scrotal sac of the male.

Soon the genital tubercle elongates somewhat and a slit, the *urogenital opening*, develops along its ventral surface. The lateral margins of the slit elevate next to form a second pair of enclosing folds, the *inner genital folds*, or the future labia minora of the female.

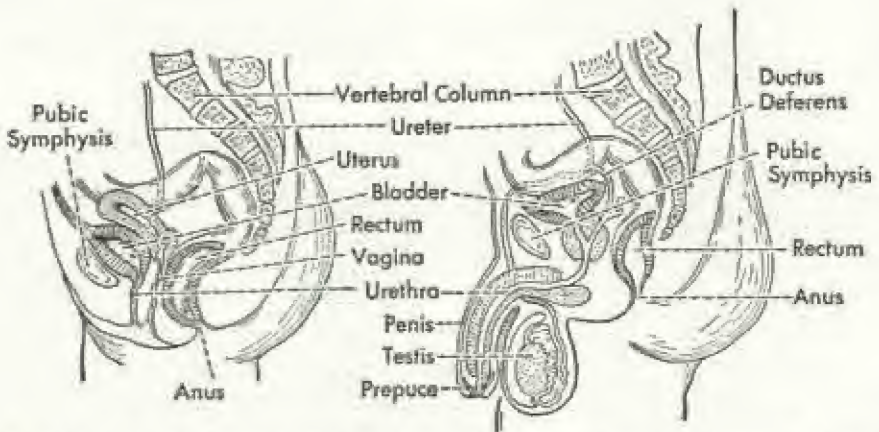


Fig. 409. Sagittal diagram of female genitalia.

Fig. 410. Sagittal diagram of male genitalia.

In the male the genital eminence, with its projecting tubercle, elongates still more into the *corpus spongiosum* and the *glans* of the penis, the urogenital slit meanwhile closing over to form the penile part of the urethra. The inner genital folds become the two *corpora cavernosa*, joining together side by side above the corpus spongiosum to complete the body of the penis, while the labio-scrotal folds draw down and grow together, forming the scrotal sac. The seamlike ridge, or *raphe*, along the midventral line of the scrotum in the adult, represents the line of fusion between these embryonic structures.

In the female the genital eminence and the genital tubercle remain comparatively undeveloped in the form of the *clitoris*, while the urogenital slit expands into the vestibular entrance to the vagina, and the two sets of folds on either side shape up into the labia minora and the labia majora.

The anterior fusion of the outer labio-scrotal folds, which make the labia majora in the female, becomes the *mons Veneris*.

So-called human "hermaphrodites" usually present intermediate embryonic features with respect to the external genitalia, as for instance, a small undeveloped penis with an unclosed urogenital slit (hypospadia), resembling the grooved cloacal penis of the turtle.

The general relations of the genitalia, both external and internal, of the two sexes in man are shown in Figures 409 and 410.

VI. PERIODICITY IN REPRODUCTION

After reaching sexual maturity, a stage which is usually less marked in the male than in the female, most animals exhibit a periodical recurrence of reproductive activity. This, as applied to the species, may be called the *breeding season*. During the breeding season the individual animal may react to a single sexual crisis, or it may undergo several rhythmical waves of sexual activity, while between breeding seasons the pairing instincts and behavior are in abeyance.

The onset of the breeding season is probably due to a variety of causes, both external and internal, differing largely in various groups of animals. There is some underlying, common ground, however, for it is apparent that the reproductive cycle of most plants and animals is timed more or less to accord with the changing seasons, and to occur at a time that is favorable for the development of the forthcoming young. This is usually the spring or early summer, particularly among insects, annual plants, and cold-blooded animals.

A host of aquatic forms, for example, respond sexually to the rising temperature of the water in the spring of the year. Ocean fishes shift in schools into warmer shallow or surface waters to spawn, while amphibians and reptiles, arousing from their winter lethargy, proceed at once to increase the census returns in their cold-blooded world.

Birds stream northward in their annual "Canterbury Pilgrimage" as soon as the cold of winter in our northern latitudes has given way to the breath of spring. At this season they show considerably more purpose than in the more leisurely fall migration. The factor of changing temperature, however, does not wholly account for the remarkable nuptial flight of birds in their spring migration.

Mammals also generally exhibit enhanced vitality and courtship behavior at the spring season. According to Bissonnette it is the gradual increase in the daily light ration which brings about this increased sexual activity of

birds and mammals. Even man, whose breeding season has been extended to include the entire year, feels the spell of spring, so that Tennyson stated a biological fact when he sang:

In the spring a livelier iris changes on the burnished dove;
In the spring a young man's fancy lightly turns to thoughts of love.

The breeding season of fishes in the valley of the Nile is during the annual period of inundation. Lungfishes, which pass the dry season burrowed inactively in the mud, breed at once when the rainy season begins, being at that time restored to activity. It is rather remarkable that hibernating animals, as well as aestivating lungfishes, when they awake starved and hungry after their dormant sleep, proceed immediately to the business of propagating the species before they attend to their own individual needs. This is a good illustration of the imperative law of reproduction, which places the preservation of the species above the welfare of the individual.

In the same self-effacing way the salmon of the Pacific Coast, when they leave the ocean for the long perilous run up rapids, waterfalls, and past countless dangers for many hundred miles to their breeding grounds in the upper reaches of the Columbia and Yukon rivers, ascetically forego feeding and devote themselves entirely to the great adventure of reproduction. It is quite probable that some internal factor, perhaps a physiological urge set in motion as a consequence of rhythmical metabolic processes, must account for the astonishing behavior of the salmon. It is certainly not entirely due to the fact that their gonads have swollen to a degree demanding immediate action, because in the "Silver Horde" of the salmon run fishes of all stages of sexual development are found. Moreover, it has been pointed out by Jacobi that the gonads of the eel, *Anguilla*, which migrates in the opposite direction, from fresh to salt water for its one breeding season in a lifetime, do not become enlarged until it reaches salt water.

The breeding rhythm of some animals is even gauged to a certain time of day. Thus amphioxus in the Mediterranean region always spawns at sundown, and the famous "pololo worm" of the South Pacific, *Eunice viridis*, produces its myriads of eggs and sperm in quantities sufficient to color the water for miles about, at daybreak of a particular day falling in the last quarter of the moon in September and October.

Many invertebrates breed once for all, the act frequently marking the end of their life cycle. Animals like most marsupials and seals breed annually; the walrus once in three years; and elephants at considerably longer intervals.

There is a curious correlation between the breeding season of bats and

a favorable time of year for the appearance of the future offspring. Pairing is effected in the fall, a mucous plug sealing the uterus after copulation so that the sperm can winter over in the vagina. After copulation has occurred the sexes go their separate ways to hibernation quarters, the males in one place, the females in another, where they literally "hang up" for the winter. Since the period of gestation in the bat is only two months, the young would normally be born during the somnolent hibernation period—an impossible state of affairs with no available insect food on the wing—were it not for the fact that fertilization is not consummated for several months after copulation, the sperm remaining viable in the vagina of the female throughout all that time.

Among mammals, the female during the breeding season passes through an *oestrous cycle*, or "heat," in which preparation is made for the fertilization of the egg. If only one oestrus occurs during the breeding season, as in the case of the bear, the animal is said to be *monoestrous*. *Polyoestrous animals*, on the other hand, are those which, like rodents, have recurrent oestrous periods following each other throughout the breeding season.

Domestication frequently works changes in the periodicity of reproduction. Many wild animals refuse to breed at all in captivity, while domestic animals, such as cattle, have been changed from a monoestrous to a polyoestrous condition. The breeding season has been greatly extended in poultry, for example, to include practically the entire year.

In the human female the breeding season is not dependent upon external factors, but continues uninterrupted from the time of puberty until the *menopause* at the age of 45 or 50 years, throughout which time the oestrus, unless interrupted by pregnancy or some abnormal condition, recurs rhythmically approximately every four weeks.

Associated with the oestrus in humankind the walls of the uterus undergo marked periodic modification, throughout the sexual life, in preparation for the possible implantation of an ovum. These changes include enlargement of the uterine glands and accumulation of fluid in the mucosa which becomes distended to several times its ordinary thickness, a state which can be maintained for only a few days. If no fertilized egg is implanted, the mucosa undergoes further changes, leading to a gradual breakdown of the superficial layers which are discharged to the outside together with secretions and 40 to 60 cc of blood, as the *menstrual flow*. Menstruation, which lasts four or five days, is followed by repair of the mucosa and the next period of preparation. Counting the first day of menstruation as the first day of the oestrous cycle, the egg is usually discharged from the Graafian follicle on the twelfth to sixteenth day. If the descending

mammalian egg meets an ascending sperm in a Fallopian tube, it may become implanted in the wall of the uterus that has been prepared for it and there undergo development. Under these conditions destructive changes in the uterine mucosa do not occur, menstruation being in abeyance during pregnancy and lactation. This monthly recurrence of the reorganization of the uterine mucosa begins and ends earlier in life in the tropics than among inhabitants of colder countries. The human menstrual cycle has been diagrammed by Corner as shown in Figure 411.

Ethnologists find indications of a former primitive breeding season in man coupled with the annual feasts and orgies of savages and in the yearly festival of the Saturnalia of classical times, when great sexual license was known to prevail.

VII. CARE OF THE YOUNG

Many instincts and dawning intelligence seem to center around the care of the young. Distinctive secondary modifications in the female have to do largely with this function. It has its beginnings in the unconscious equipment of eggs with nutritive materials and in the provision by the female of a sheltering uterus or brood sac of some kind. Later in evolution parental care may take the form of building nests in which to incubate eggs after they have been laid, and of behavior that supplements the helplessness of the newly hatched or born.

In higher animals there is a prolonged period of dependence upon the parents, after hatching or birth, which makes "schooling" possible through association with the parents. The relation is a reciprocal one, for the child or offspring is an educator as well as the parent. Coöperation, not competition, is the key to family life exhibited by man and the higher animals. In this way the traditions and acquired wisdom are handed on among animals as soon as an adequate vehicle by way of brain equipment is elaborated for it.

The lower animals, on the other hand, never have any schooling. They are supplied once for all with a single "box of tricks," or instincts, and as soon as they come into the world they know as much as their parents or as much as they need to know to fill their niche in nature. They never can experience the joy of learning from their parents or others of their kind and in the majority of instances they never even encounter their parents.

A prolonged dependence upon parental care is a mark of superiority, since it furnishes the soil in which budding intelligence may grow and flourish.

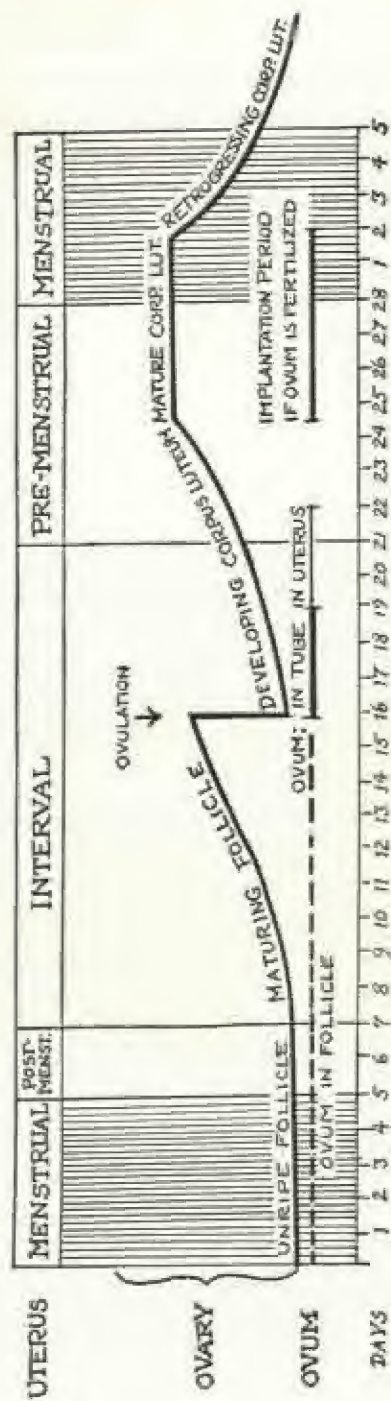


Fig. 411. The course of events in the human menstrual cycle according to G. W. Corner. (By permission of J. & A. Churchill, Ltd.)

The dominance of mankind is correlated with the fact that the education involved in family life is extended over relatively so long a time. In the case of modern man, children do not gain independence from their parents, in the most fortunate instances, until at least one third of the entire span of life is past.

Involuntary Regulation—Glands of Internal Secretion

I. IN GENERAL

There are two general devices, nervous and chemical, for effecting coördination within the animal body. The former is somewhat like a telegraph system, whereby messages are conveyed from one point to another without material transfer, while the latter is more like the parcel post, in that substances produced by certain organs are distributed through the blood system to other parts of the body, where they bring about results affecting the entire organism.

The chemical regulators of the body have their origin in glands. Some glands, for example those of the digestive tract, are provided with ducts and furnish chemical substances called *enzymes*, that are indispensable agents in the utilization of food materials. Others have no ducts and can only deliver their products by the agency of blood vessels with which they are in intimate contact. These are the *endocrine glands*, or "glands of internal secretion."

The chemical substances that they elaborate from the blood are termed *hormones*, which like enzymes may act in very small quantities, suggesting that they are catalytic in action, or in other words that they hasten chemical action without themselves undergoing any permanent change. They not only bring about functional results by maintaining chemical equilibrium within the body, but they also play an important part in developmental processes. The term hormone means "exciter," which indicates in general the character of this kind of intramural messengers. Some ductless glands produce substances, however, that act as restraining bridles rather than as stimulating spurs, and such glandular products are called *chalones* in distinction to *autocoids*, or hormones proper.

The total mass of human endocrine glands all rolled together would

equal, according to an eminent English biologist, a parcel small enough to "go in a waistcoat pocket," yet their importance is so great that, with the advance of knowledge gained within the present century largely through pathological studies and animal experimentation, the new biological science of *Endocrinology* has arisen, absorbing the attention of a small army of specialists and possessing a rapidly increasing literature all its own.

The glandular system involves considerably more than the ductless glands, since there are glands having ducts, for example the pancreas and the gonads, that in addition deliver hormones directly into the blood, as well as substances through ducts. Moreover, certain substances not produced by glands act also through the medium of the blood in a manner similar to that of the hormones. Carbon dioxide, for instance, resulting from the activity of muscle tissues, which is transported by the blood stream to the respiratory nervous center in the medulla where movements essential to breathing are regulated, belongs in this category.

The endocrine glands are subject to great variation and, although largely interdependent, their hormones, carried everywhere that blood flows, are effective only upon certain specific organs. They are like keys to fit particular locks but not master keys to fit all locks.

Upsets in the balance of endocrine activities result in various pathological manifestations, while the loss of certain of these glands of internal secretion results fatally. The interlocking endocrine system among other things is responsible, in part at least, for (1) the time, order, and rate of organic development; (2) metamorphosis in amphibians; (3) adaptive coloration in certain larval salamanders; (4) the development of secondary sexual characters; (5) a considerable part of visceral control; and (6) many phases of behavior, particularly the "emotions" that contribute so much to the psychic life and to the determination of "personality."

The possibility of controlling and regulating the functions of the ductless glands has opened a new broad field for experimentation and medical practice, with the inevitable and often deplorable accompaniment of much unfounded speculation and quackery.

No ductless mass of cells which is not muscular, nervous, or skeletal can escape the suspicion of being involved in the endocrine system. For example, the spleen has been suspected of endocrine affiliations although the only functions definitely shown for it have to do with the circulatory system. Substances similar to vertebrate hormones, associated with such phenomena as color changes in crustaceans and metamorphosis of insects, have already been discovered in invertebrates despite limited investigations along this line. Plants have also been found to produce certain substances that act after

the long-arm method of hormones upon structures distant from the point of their elaboration.

For convenience in description, the principle endocrine structures of the vertebrate body (Fig. 412) may be grouped into four categories according to their general location: (1) *pharyngeal* (thyroid, parathyroid, and associated glands); (2) *cranial* (pineal, anterior and posterior pituitary); (3) *sexual* (testes, ovaries); and (4) *abdominal* (pancreas, intestinal, adrenals).

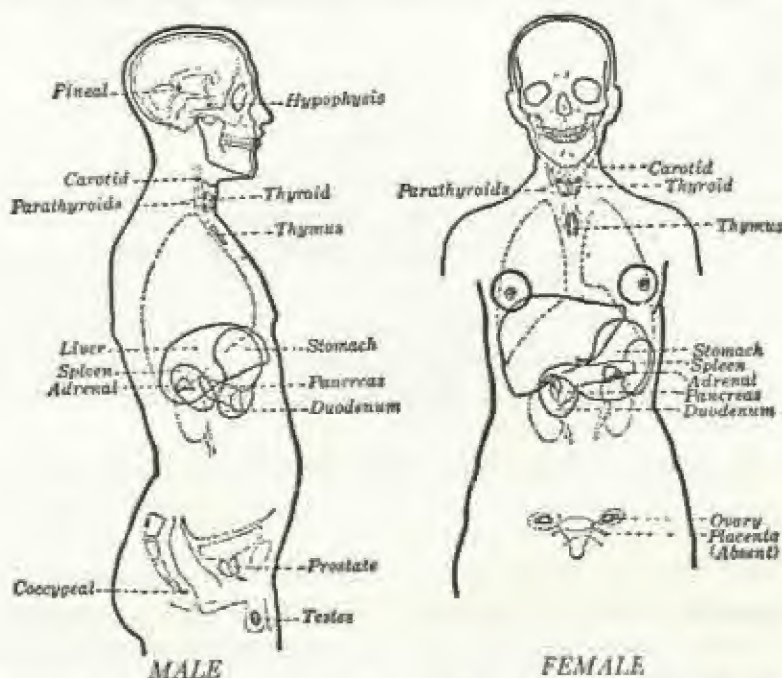


Fig. 412. Diagram of the endocrine system. (From chart in *Endocrinology and Metabolism*, edited by L. F. Barker. D. Appleton and Co.)

II. PHARYNGEAL GLANDS

1. Thyroid

The vertebrate pharynx is a region of much evolutionary modification. One of the oldest structures found there is the *thyroid gland*, foreshadowed in the *endostyle* of tunicates and amphioxus (Figs. 10 and 15), where it is an open groove in the floor of the pharynx, lined with mucus-producing cells and supplied with long cilia (Fig. 319).

In other vertebrates there is a similar evagination of endodermal tissue from the floor of the pharynx between the first pair of gill pouches (Fig.

413) that corresponds to the endostyle. It begins to develop very early in man, when the embryo is about $1\frac{1}{2}$ mm. in length, and does not fail to put in its appearance in every vertebrate. It soon loses its connection with the



Fig. 413. Diagram showing the origin of various branchial epithelial structures, I-V, branchial pouches. (After Kohn.)

pharynx, however, and becomes a ductless gland, made up of a mass of closed follicles, surrounded by connective tissue.

The duct of this embryonic thyroid gland still remains open during the "amocoetes" stage of the lamprey eel but is obliterated in other vertebrates. In man it disappears by the eighth week of fetal life, although its place of former opening is marked by the *foramen caecum* at the base of the tongue (Fig. 233).

The thyroid grows slowly but steadily throughout the prenatal period, until at birth its weight is about 0.125 per cent of the total weight of the body. After birth, while its actual weight still increases, its relative weight decreases, so that eventually in adult life it normally has a weight of about 40 grams, being somewhat heavier in the human female than in the male.

The blood supply of this gland, which comes from both the carotid and the subclavian arteries, is very generous. Wiedersheim states that it may equal or even exceed that of the brain.

In most fishes the thyroid gland is composed of several groups of loose follicles scattered along the ventral aorta, but in amphibians, reptiles, and birds, although double embryonically, it becomes increasingly compact, and in mammals finally assumes a bilobed shape, with flattened *lateral portions* joined together by a connecting *isthmus* (Fig. 414).

The shifting of the thyroid gland from its original anterior position in the floor of the pharynx to a more posterior situation near the upper part of the trachea is made possible because it is in no way anchored at the point of origin by a hampering duct. Every time the act of swallowing takes place it moves up and down with the larynx.

Obviously there has been phylogenetic change of function in this organ. From a device, partially glandular, useful for the mechanical manipulation of food particles taken in with water, it has become an endocrine structure, producing a hormone affecting the oxidation processes, and consequently the rate of living. Davenport aptly says of the endocrine glands generally, "They are made up mostly of odds and ends of more or less discarded organs, the gonads of course excepted."

The hormone produced by the thyroid gland is *thyroxin*, a compound rich in iodine, which has been not only chemically isolated and crystallized, but also artificially synthesized. Kendall of the Mayo clinic had to use 6550 pounds of fresh thyroid tissue to get one ounce of pure thyroxin.

When introduced into an animal either with food or by subcutaneous or intravenous injection, it may produce marked results. Tadpoles, for example, fed with thyroid gland, change into tiny frogs the size of a fly without "growing up." If instead they are thyroidectomized, they grow into large tadpoles without metamorphosis.

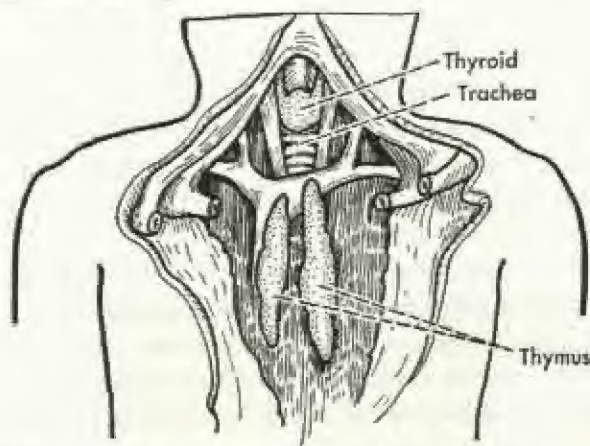


Fig. 414. Thyroid and thymus in a child one month old. (After Olivier.)

Human beings with a deficient thyroid apparatus while still young children may develop abnormally into unfortunate defectives called *cretins*, having retarded or imperfect physical and mental development. Thyroid-deficient adults may suffer from *myxedema*, a condition characterized by over-growth of connective tissue or fat, loss of hair, weak muscular development, oedematous skin, impoverished blood, deficient sexuality, lowered metabolism, nervous depression, and frequently impaired mentality. Fortunately this condition may be relieved or removed entirely, when taken in time, by the proper administration of thyroid extract.

An excessive development of the thyroid gland results in abnormally increased oxidation and manifestations of disease such as *exophthalmic goitre*, or *Graves' disease*, in which the patient becomes extremely nervous and thin, exhibiting characteristically protruding eyeballs. This is a serious progressive disturbance not to be confused with *common goitre*, an enlargement of the thyroid due to deficiency of iodine, an essential constituent of thyroxin. Common goitre usually results from living in a region like Switzer-

land or the Midwest in the United States where the soil, and consequently food materials derived therefrom, lack iodine.

The periodic administration of a small quantity of sodium iodide to the school children of the Middle States far removed from the sea shore, has resulted in the reduction of the occurrence of common goitre in those regions.

The thyroid gland has been aptly called the "pace setter," or metabolic regulator of the body.

2. Parathyroids

Budding off embryonically from the walls of the gill pouches are various epithelial structures that later become glandular. Among these are the *epithelial bodies*, *thymus glands*, *ultimobranchial bodies*, and *parathyroids*.

In cyclostomes there are seven separate pairs of these structures which form the epithelial bodies, situated in the ventral region of the gill pouches. They are lacking in teleost fishes, but from the amphibians on there are usually present at least two pairs of glandular structures that are probably homologous with epithelial bodies, since they arise like them from the dorsal region of the gill pouches, particularly from the third and fourth pairs. Epithelial bodies, which have been identified in lizards, some birds, and many mammals, are known as *parathyroids* (Fig. 413), because they eventually assume a position either in direct contact with, or close to, the thyroid gland (Fig. 415).

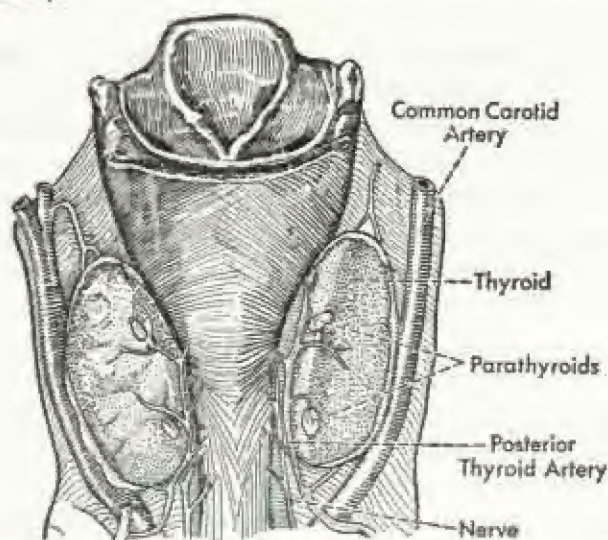


Fig. 415. The thyroid and parathyroid glands shown from the dorsal side. (After Halsted and Evans.)

In man they are small brownish yellow encapsuled bodies, two pairs of which usually lie embedded in the median dorsal surface of the thyroid gland on either side. Still others may occur in the thyroid or farther down the sides of the neck, even as far posterior as the thymus.

Although in man their combined weight is less than half a gram and their massed size a few millimeters in diameter, they are indispensable to life, since their complete removal always results in death. Children's convulsions are found to be correlated with parathyroid deficiency, and the fatal tetanic fits, which almost invariably followed thyroidectomy in the earlier days, are now known to be due, not to the removal of the thyroid gland itself, but to the accidental extirpation of the parathyroids during thyroid operations. The hormones produced by the parathyroid glands play an important rôle in the vital calcium metabolism of the body.

3. Thymus

The *thymus glands*, like the parathyroids, have a multiple origin, but come from the ventral region of the gill pouches instead of the dorsal region (Fig. 414). Although present in all vertebrates, they remain epithelial in character in some fishes, while in higher forms they become lymphoid and highly vascular. The different embryonic elements of the thymus frequently fuse together to form continuous masses of tissue down either side of the neck.

In mammals including man, the thymus gland is principally derived from the posterior epithelium of the third gill pouch. It reaches its actual maximum in size at about the time of puberty, although its greatest relative size is attained much earlier, in infancy.

The total removal of the thymus is not fatal. Although its function is not known, Gudernatch has shown that in tadpoles fed upon thymus growth is accelerated and metamorphosis is delayed, an effect just opposite to that obtained when thyroid is employed as food.

Recent researches have by no means sustained the hypothesis that the thymus is an endocrine gland. Hoskins summarizes the present state of our knowledge by saying, "In all probability the organ is of significance in the physiological and pathological processes, merely by virtue of its lymphoid character."

4. Ultimobranchials

The *ultimobranchials* (Fig. 413), as their name indicates, are the most posterior of the series of pharyngeal derivatives which may be suspected of endocrine activities. They arise behind the fifth pair of gill pouches. Only the

left ultimobranchial body develops in lizards (Fig. 416), and their occurrence in birds and mammals is doubtful. The ultimobranchial bodies in function may be connected with other lymphoid structures throughout the body, like the *tonsils*, which are also pharyngeal derivatives.

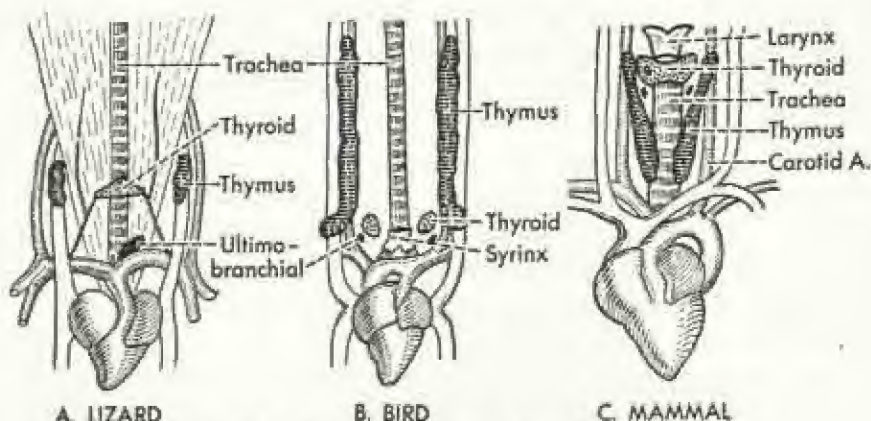


Fig. 416. Pharyngeal glands. (After DeMeuron.)

III. CRANIAL GLANDS

The pituitary and pineal bodies are two structures on the ventral and dorsal sides of the brain respectively, which require special consideration in this connection.

1. Pituitary

The *pituitary* complex has been termed the "master gland" in the endocrine system because the activity, particularly of the thyroid and of the gonadal glands, is interlocked with and initiated by this gland. It has been aptly called by the French physiologists "*l'organ enigmatique*."

It is a compound structure of double origin, located most inaccessibly just behind the optic chiasma in the space between the roof of the mouth—roof of the nasal cavity in amniotes—and the ventral side of the brain. In man and higher vertebrates it lies ensconced in the *sella turcica*, which is a cradle-like space hollowed out in the sphenoid bone of the cranial floor. Its dual origin is due to the fact that a part of it is composed of an up-pushing growth from the roof of the stomodaeum which meets and becomes incorporated with a down-pushing extension from the floor of the brain. The stomodaeal portion is the *adenohypophysis*, the nervous portion the *neurohypophysis*. Phylogenetically it is very old, being represented in all living vertebrates.

Its relative size decreases from the lower to the higher vertebrates. In adult man it is "about as large as a hazel nut," or rather less than a cubic centimeter in bulk, weighing normally 0.5 gram. In myxinoids it discharges its secretions directly into the pharynx, but otherwise throughout the vertebrate series it has become a ductless gland, concerned solely with internal secretion.

The name "pituitary," meaning phlegm, was given to this structure because Galen and the early anatomists, who had already discovered it, thought that it produced nasal secretions.

The pituitary body consists primarily of three parts: one posterior, *pars nervosa*; one intermediate, *pars intermedia*; and one anterior in position, *pars anterior*. In some vertebrates there is distinguishable, in addition, a so-called *Uebergangsteil*, containing transitional types of cells between those characterizing the anterior lobe and the posterior lobe, as well as a *pars tuberalis* associated mostly with the anterior lobe. The *pars tuberalis* has been found in amphibians and mammals but is absent in cyclostomes, some fishes, and most reptiles.

(a) **Posterior Lobe.**—The *posterior lobe*, or *pars nervosa*, of the adult mammal consists of a neural portion derived from the brain (Fig. 417). It is formed from the *infundibulum*, which is a downgrowth of the *diencephalon* of the brain (see Fig. 630).

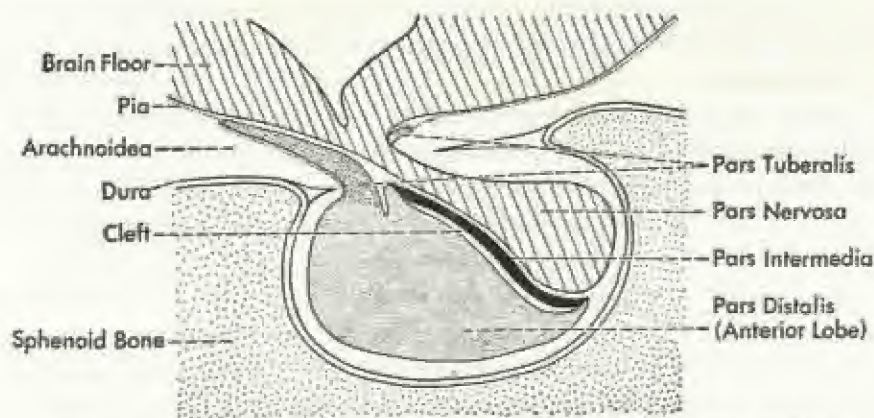


Fig. 417. Diagrammatic sagittal section of the hypophysis. The cleft is the remains of the cavity of Rathke's pouch. (After Atwell.)

The hormone *pituitrin*, produced by the posterior lobe of the pituitary, has to do with fat formation, the production of urine, and the development of the sexual apparatus, the whole structure in the female increasing in size

during pregnancy. Pituitrin stimulates smooth muscle cells to contraction. It therefore diminishes the caliber of the arterioles, thereby bringing about both an increase in blood pressure and a reduction in urine secretion. It is used in obstetrics to accelerate the contraction of the uterus and thereby hasten *parturition*, the delivery of the child. When administered at a later stage it assists the uterus to return to its resting condition.

By giving pituitrin to pigeons, Riddle succeeded in bringing about a sort of abortion in these birds, since it caused them to lay eggs at an exceptionally early stage of development.

(b) **Intermediate Lobe.**—The *pars intermedia* is the least vascular part of the pituitary mass, but it is nevertheless apparently secretory in character. It is well developed in lower vertebrates and in all vertebrates it separates the anterior lobe from the *pars nervosa*.

Both intermediate and anterior lobes have a common origin by way of an ectodermal evagination, *Rathke's pouch*, which pushes up from the roof of the mouth and eventually becomes cut off after coming in contact with the posterior neural lobe. Cushing compares the whole pituitary apparatus to a ball held in a boxing glove, in which the ball itself represents the posterior lobe, the cover on the ball the *pars intermedia*, and the glove the enveloping anterior lobe, which increases in size and importance in the ascending vertebrate series.

(c) **Anterior Lobe.**—The *anterior lobe*, which is the largest part of the pituitary apparatus except in cyclostomes and teleosts, is made up of at least three kinds of cells that stain differently and consequently are of diverse chemical nature.

On the periphery are *basophil cells*, which take basic stains readily. In the center are *acidophil cells* amenable to acid stains, while *chromophob cells*, that are not easily affected by either basic or acid stains, are scattered throughout the structure, completing the "ABC" trinity (acidophil, basophil, chromophob) of cell components.

The anterior lobe produces several hormones at least one of which regulates growth while others stimulate the gonads (*gonadotropic hormone*), the thyroid (*thyrotropic hormone*), or the adrenals. Insufficient *growth hormone* results in *dwarfism* while excesses of this substance bring about *gigantism* or, if produced after maturity, a condition known as *acromegaly*, the excessive growth of certain bones and joints.

The complete removal of the pituitary probably results in death, although the difficulty of access to it, and the resultant unavoidable injury to neighboring brain tissues, may be the reason for fatal results frequent in operations upon it.

2. Pineal Body

On the dorsal side of the brain and completely concealed in the higher vertebrates by the dominating growth of other parts, is a small stalklike evagination of the brain wall called the *epiphysis*, or *pineal body*. In fact one or another of three different structures, the *paraphysis*, *parietal organ*, and *epiphysis* (Fig. 418), all of neural origin and easily confused as to their probable homologies, may be located in this part of the brain.

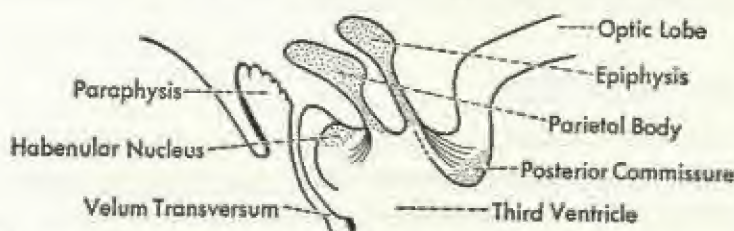


Fig. 418. Evaginations of the epithalamus shown in sagittal section. Only the roof of the brain is shown. (After Johnston.)

The most anterior of these structures is the *paraphysis*, which lies directly in front of the *velum transversum* at the junction between the cerebral hemispheres and the diencephalon. The *parietal organ* is sensory in character rather than glandular, and in *Sphenodon* and some other lizards it becomes a median eye-stalk of more or less efficiency, reaching the top of the head under a window-like foramen that pierces the skull. The *epiphysis* and the *parietal body*, although arranged in tandem fashion whenever both are present, as in cyclostomes, were probably once paired structures lying side by side. The *epiphysis* is the more constant of the two structures, being almost universally present in vertebrates. Originally probably a sense organ, it has become glandular and even fibrous in character.

The *pineal body* in mammals is the persisting proximal or basal portion of the *epiphysis*. Its shape resembles somewhat that of a pine cone, from which circumstance it takes its name. Relatively larger in children than in adults, and attaining its best development in man at about seven years of age when involutionary changes begin to appear, it measures only about 8 mm. in length.

The pineal body has been known to anatomists since early times and has always been a source of much curiosity and speculation. Repeated attempts have been made experimentally to discover its activity and to ascertain significant structural modifications associated with abnormal conditions in the development of this organ, but the results have been conflicting and disap-

pointing. The fact that it is a highly vascular structure, frequently lobulated like a gland and containing secreted pigment, has raised the suspicion that it may have some endocrine function, but its extirpation does not seem to be followed by unmistakable physiological consequences, except that sexual maturity is somewhat hastened when it is destroyed. While it is no doubt a degenerate structure, it may possibly be of physiological importance with some obscure endocrine function, yet hardly more has been proved with regard to it today than when Descartes (1596-1650) three centuries ago guessed that it was the "seat of the soul."

IV. SEXUAL GLANDS

As already pointed out in the preceding chapter, the gonads, or primary reproductive organs, not only furnish either sperm cells or eggs, but they are also glands of internal secretion.

Whenever castration occurs before puberty, the so-called secondary sexual characters fail to develop. It has been shown that this result is due not to that part of the testis or ovary which produces the sperm cells or eggs, but to certain interstitial glandular cells of endocrine function, called "puberty glands" (Steinach).

1. Male Gonads

There are three kinds of cells in the testis, namely, spermatogenic, Sertoli cells, and interstitial cells. The first two make up the walls of the seminiferous tubules, while the interstitial cells are grouped around the blood vessels in the spaces between the tubules. They form before the germ cells do and respond differently to various stains, thus indicating their specific character. Moreover, they do not succumb to the lethal effects of X-rays as quickly as do sperm cells.

When an animal is deprived of the hormones produced by the interstitial tissues of the testis, there is a tendency for distinctly male characteristics, such as the horns of the stag, the plumage colors of male birds, the distribution of hair that marks the male mammal, and particularly male behavior in courtship, to revert to a neutral condition. Interstitial glandular tissue, however, is not found in the testes of all vertebrates, and it is equally true that many vertebrates are without secondary sexual characters.

2. Female Gonads

Small groups of interstitial cells were discovered in the ovary by Pflüger as early as 1863, but subsequent study thus far only goes to prove that they

lack the morphological individuality of the interstitial testicular cells and may not belong to the same endocrine category. In the ovaries of certain mammals, including man, at least two hormones are produced, *estrogen*, formed by developing *Graafian follicles*, and *progesterone*, elaborated in the *corpus luteum* which is formed in the follicle, after the liberation of the egg, by proliferation of the cells of the *zona granulosa*.

Estrogen is associated with the development of secondary sexual characters and, after puberty, regulates oestrous and, in Primates, the menstrual cycle. Progesterone initiates the changes preparatory to implantation of the ovum and also may inhibit oestrous and menstruation, which does not occur when the corpus luteum persists as in pregnancy and some pathological conditions. Apparently degeneration of the corpus luteum, gradually cutting off the supply of progesterone near the end of gestation, is associated with the onset of milk production, or *lactation*, and the sensitizing of the uterine muscles to pituitrin, which leads to parturition. Pearl and Boring have also demonstrated the presence of *lutein cells* in the ovary of the hen, although the mammalian functions just enumerated do not occur in birds.

It will be noted that whatever endocrine tissues are present in either the ovaries or the testes serve in the long run the same general purpose of maintenance of the species as do the primary sex cells produced in the gonads, since secondary sexual characters contribute indirectly to the general function of mating and reproduction.

V. ABDOMINAL GLANDS

I. Adrenals

The *adrenals*, or *suprarenals*, are compound endocrine glands peculiar to vertebrates. In man they are two small but important structures, weighing only eight or nine grams each, which fit "like cocked hats" over the anteromesial ends of the kidneys (Fig. 419). They are enclosed in delicate but firm capsules of connective tissue that separate them from the kidneys to which they are closely adherent but of which they are physiologically independent. They are relatively the most richly vascularized organs of the body, since five or six times their intrinsic weight of blood passes through them per minute. They are somewhat smaller in the female than in the male, and frequently in the same individual the one on the right is smaller than that on the left.

Although discovered long ago by Eustachius, who has so many other anatomical discoveries to his credit, their significance and importance as

endocrine glands has only recently been made clear by Cannon and others. The first hormone to be isolated in pure form, *adrenalin*, or *epinephrin*, was obtained from these glands. This substance, which has also been chemically synthesized, is known to chemists as *ortho-dioxy-phenyl-ethanol-methylamine*.

In structure the adrenals consist of an outer *cortex* and an inner *medulla*. These two parts are not only morphologically and embryonically distinct, but are also chemically and physiologically different.

In origin there is a close relationship between the inner medullary cells of the adrenal glands, which produce the adrenalin hormone, and the sympathetic nervous apparatus. When migrating cells of the central nervous system become detached during development and move out to establish the sympathetic ganglia, they are of two kinds, although indistinguishable without recourse to differential staining. Some of them, *sympathoblasts*, become involuntary neurons of the sympathetic ganglia, while others, *chromaffinoblasts* although of common origin with the sympathoblasts, are transformed into so-called *chromaffin cells*, since they show a special affinity for chromic-acid salts, taking on a distinctive brownish color in the presence of the latter.

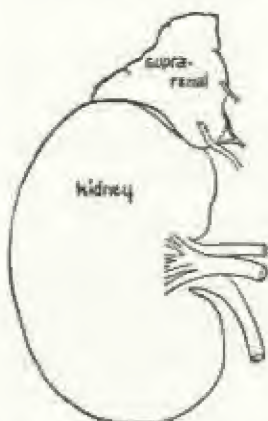


Fig. 419. Human supra-renals. (After Heitzmann.)

These chromaffin cells form glandular endocrine masses, and the extent to which they may be stained by chromium compounds is proportional to the amount of adrenalin which they are producing at the time.

It is the chromaffin derivatives of the coeliac plexus in the autonomic nervous system which give rise to the medulla of the adrenal glands. Chromaffin tissue, however, is not confined to the adrenals, but may be associated with any of the sympathetic plexuses or ganglia, forming *paraganglia*, or *chromaffin bodies*, of various sorts. These are frequently associated with concentrations of capillaries, as for example in the *carotid glands* at the junction of the internal and external carotid arteries, and the so-called *aortic bodies of Zukerkandl*, two or three in number, which are near the aorta in the human fetus and during early childhood.

In fishes the chrome-staining adrenalin-secreting tissue is not concentrated into a medulla within a cortex, but is a diffuse double row of groups of cells associated with the trunk-line chains of sympathetic ganglia. During the phylogenetic ascent of the vertebrate series, the neuron elements of this

partnership increase in number and importance, while the chromaffin cells diminish.

In addition to the chromaffin bodies in fishes there are, lying between the straplike kidneys, two elongated masses of tissue, derived from the coelomic epithelium, and named from their position the *interrenals* (Fig. 420). These are destined to form the *cortical part* of the future adrenals.

A transitory evolutionary stage is presented in amphibians, in that the original close connection between the chromaffin cells and the sympathetic ganglia is partially lost, and the interrenal tissue comes into close contact with and begins to envelop the chromaffin bodies. This new association becomes still more intimate in reptiles and birds, but it is only in mammals that a definite chromaffin medulla becomes established inside an interrenal cortex. The lower the species within the mammalian line, the greater is the relative amount of the cortical component.

There are various theories as to the function of the chromaffin system. It is known that when adrenalin is injected into an animal there is a sudden, decided, but comparatively brief rise in blood pressure; the heart beat is steadied, becoming slower and more powerful; there is a quick increase of emergency sugar-fuel (*glycogen*) poured into the blood stream; and the muscles, particularly the involuntary muscles that are supplied by sympathetic nerves, are thrown at once into their most efficient state of tonus. Thus, in emergencies, the temporary "strength of desperation" is furnished by the adrenalin, and fatigue is for the time banished.

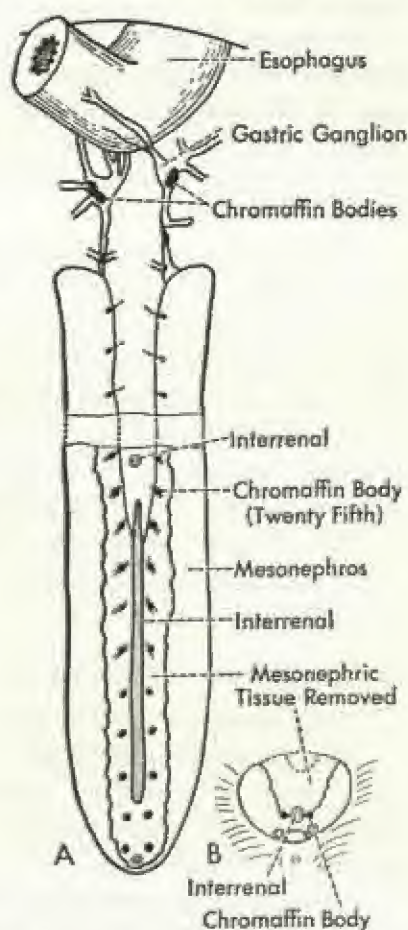


Fig. 420. The interrenals and chromaffin bodies of *Squalus*. A, ventral view, showing these structures exposed by removal of part of each mesonephros. B, cross section showing positions of glands and extent of part removed in A. (After Lutz and Wyman.)

Although minute quantities of this hormone are essential to the normal process of metabolism, it is not supplied continuously to the blood in any great quantity, but only as occasion demands to meet some transient physiological crisis.

A separate hormone, *cortin*, is developed from the adrenal cortex, either singly, or as a group of hormones having a common base. It plays an important rôle in carbohydrate metabolism and aids in the utilization of certain *vitamins* which are indispensable components of foods. According to Swingle, cortin has to do with maintaining the acid-base equilibrium within the body.

At least one pathological condition, *Addison's disease*, is definitely correlated either with deficiencies or lesions of the adrenals, especially those arising from tuberculosis. This disease, which was first described a century ago by Addison from Guy's Hospital in London, is characterized on the part of the patient by muscular weakness, low blood pressure, digestive disturbance, and the appearance of peculiar bronze patches upon the skin. Although the course of the disease may be somewhat modified by the administration of cortin, a fatal termination seems to be the usual outcome.

The adrenals undergo precocious growth, reaching their largest relative size in man about the third fetal month, when they are as large as the neighboring kidneys.

2. The Islands of Langerhans

The *pancreas* is another gland compounded of two kinds of tissues.

The pancreatic cells proper are grouped about a system of drainage ducts, and the substances elaborated by them are important digestive enzymes, which escape through these ducts into the small intestine, as described in Chapter XI.

Throughout the vertebrates there appear in isolated groups between the cells of this glandular system distinct interalveolar cells arranged as anastomosing cords alternating with *sinusoids* and forming rounded masses (Fig. 270). They have no outlet by way of ducts for the substances that they produce, and consequently resort to the endocrine method of disposal through the blood system. Such interstitial masses of endocrine tissue are known as the *islands of Langerhans*.

It has been ascertained that *insulin* (*insula*, island), the hormone which they produce, affects carbohydrate metabolism by regulating the use of sugar within the body. Disturbances in this function lead to the pancreatic disease of *diabetes*, which is characterized by an excess of unoxidized sugar in the blood and urine. This condition is being effectively treated by the use

of insulin, which was first successfully isolated by Banting and Best in 1922.

In fishes the islands of Langerhans are condensed into large superficial lumps that may be easily severed from the remaining pancreatic tissue, but in higher forms the characteristic grouping into small insular masses occurs.

It is estimated that in the pancreas of the guinea pig there may be as many as 25,000 "islands," while in man their number may exceed a million. They are rather more abundant in young animals than later in life. In man they make their appearance first in embryos about 54 mm. long.

PART THREE

THE MECHANISM OF MOTION AND
LOCOMOTION

The Skeleton

I. THE RÔLE OF THE SKELETON

In Ezekiel's famous vision of bones as described in the Bible, "there were very many in the open valley and, lo, they were very dry," but it should be recalled that the prophet bravely addressed himself to the bones as follows: "I will lay sinews upon you, and will bring up flesh upon you, and cover you with skin, and put breath in you, and ye shall live."

To make dry bones, wherever found, live again is exactly what biologists have been trying to do ever since, with the gratifying and somewhat surprising result that the study of bones, with their many transformations and homologies, turns out to be one of the most animated chapters in all comparative anatomy.

The student of anatomy usually begins with *bones*, since they are easily available, can be used over and over again, and are not unpleasant to handle. If he succeeds in passing undismayed through this valley of dry bones, he feels himself initiated and ready to go on with what are generally regarded as the livelier aspects of the subject.

The vertebrate skeleton is considerably more than dry bones that furnish a scaffolding for the softer parts of the body. There are at least five specific uses to which the skeleton is put, namely, (1) to give protection to other parts; (2) to make a framework for the support of the body; (3) to furnish a firm as well as an adequate surface for the attachment of muscles; (4) to provide suitable leverage for locomotor purposes; and (5) to keep up a continuous manufacture of red blood corpuscles in the marrow tissue within the cavities of the bones.

Protection is one of the earliest of skeletal functions to develop phylogenetically, being found wherever life teems, even in plants. Among invertebrate animals it reaches its most efficient elaboration in the limy shells of mollusks and the chitinous armor of arthropods. Traces of the external skeleton of invertebrates in the form of scales, nails, and various hard corneal

structures still persist among vertebrates, although here the function of protection is principally taken over by the living endoskeleton as represented by the boxlike cranium around the brain, by the neural arches of the spinal column enclosing the nerve cord, and by the thoracic basket which provides sanctuary for various important soft organs (Fig. 421).

The skeleton *as a support*, that is, as an internal living scaffolding on the outside of which muscles are arranged, instead of a lifeless external armor, is a brand new idea peculiar to vertebrates and is of far-reaching evolutionary significance in the animal kingdom.



Fig. 421. Diagram to show the reciprocal relations of the functions of protection and support in the skeleton. The trend of evolution is in the direction of the arrow.

Obviously, a living growing endoskeleton avoids the limitations of size imposed by invertebrate exoskeletons. Its capacity for continuous growth and adaptation keeps easy pace with the increasing demands of the enlarging organism as no non-living outside skeleton could do. During the Mesozoic "Golden Age of Reptiles," while arthropods and mollusks were still imprisoned with clumsy unyielding armor, Mother Nature was reveling in the possibilities furnished by a living internal skeleton among her emancipated vertebrates. Gigantic dinosaurs, plesio-

sauurs, iguanodons, and theromorphs, together with all their monstrous and bizarre kith and kin that have long since vanished, literally lifted tons of flesh into the air upon majestic bony scaffoldings, which today are a source of never-ceasing wonder to the visitor of museums where they are exhibited. No arthropod or mollusk of such astonishing dimensions as these extinct reptiles displayed is conceivable. There still remain colossal elephants on land and enormous whales in the oceans as living examples of how far it is possible to go in the matter of body size, when an adequate internal support is provided.

Since sufficient solid surface must be conveniently placed so as to give proper *foothold for the muscles*, the skeleton arises to meet this necessity. Not all muscles require the aid of bones. Those responsible for peristaltic movement in the intestinal wall, for pulsating arteries and the throbbing heart, as well as various sphincters, such as those that close the anus or pucker the whistling lips, are not directly attached to hard skeletal parts. Most muscles, however, through the mediation of tendons do have bony anchorage both at their origin and at their insertion.

The skeleton of the flying bird furnishes an excellent illustration of what is meant by having a relatively large solid expanse for muscle attachment. In spite of the necessity in every flying machine for economizing weight, it

will be seen (Fig. 422) that in the bird's skeleton there is a relatively enormous breastbone, with a thin "keel" at right angles to it, which practically doubles the expanse of surface available for the attachment of flying muscles without adding very much to the total weight. The ribs of the bird are much flattened also to make the same amount of bone furnish the largest possible surface, while the swollen ends of the leg bones have a considerably larger relative expanse available than do corresponding mammalian bones.

In man conspicuous skeletal surfaces are to be found on the innominate bones of the pelvis, the muscles of which have to do with maintaining an upright posture, as well as on the broad shoulder blades that furnish anchorage for the muscles operating the swinging arms.



Fig. 422. Skeleton of a bird, showing large surfaces for muscle attachment. (After Bradley.)

In the evolutionary emergence of vertebrates from water to land and air, *levers* in the form of legs and wings appeared as organs of locomotion. Such specialized levers are unnecessary for a fish which moves about by wagging the entire body sidewise in a watery medium sufficiently resistant to make lateral strokes effective. The difference in density between water and air is so great, however, that a mechanism moving successfully by sculling in water would prove entirely ineffective when operated in the thin and comparatively non-resistant medium of air.

One of the first steps in the evolution of locomotion upon land, therefore, has been the elevation of the elongated body from the ground by means of proplike legs to minimize the amount of frictional surface and at the same time to provide a system of skeletal levers upon which the muscles of locomotion may act in propelling the animal forward.

In birds the body is poised upon the hind legs alone, while the fore legs are released from terrestrial locomotion, becoming transformed into wings for flight through air. In both cases a system of bony locomotor levers is emphasized.

The last of the five general uses of the skeleton, that of the *manufacture of red blood corpuscles*, is accomplished, in mammals at least, by means of vigorous marrow tissue within the hollow bones.

Four general kinds of skeletal tissues may be recognized in vertebrates,

namely, notochordal, connective, cartilaginous, and bony. These tissues have been briefly described in Chapter VII.

II. JOINTS

Whenever two bones come in contact with each other during growth processes, a *joint* is formed. It may be a rigid immovable joint, *synarthrosis*, as between skull bones, characterized by edge-to-edge *sutures* that interlock the bones firmly with one another (Fig. 423), or the different embryonic



Fig. 423. Sutures. A, surface view; B, cross section of interlocking suture; C, cross section of squamosal suture.

bones may even fuse solidly together, thus obliterating the sutural joints entirely and resulting in a decrease in the total census of bones composing the adult skeleton. An exception to these *interlocking sutures* of the skull is the *overlapping* type between the squamosal bone and its neighbors.

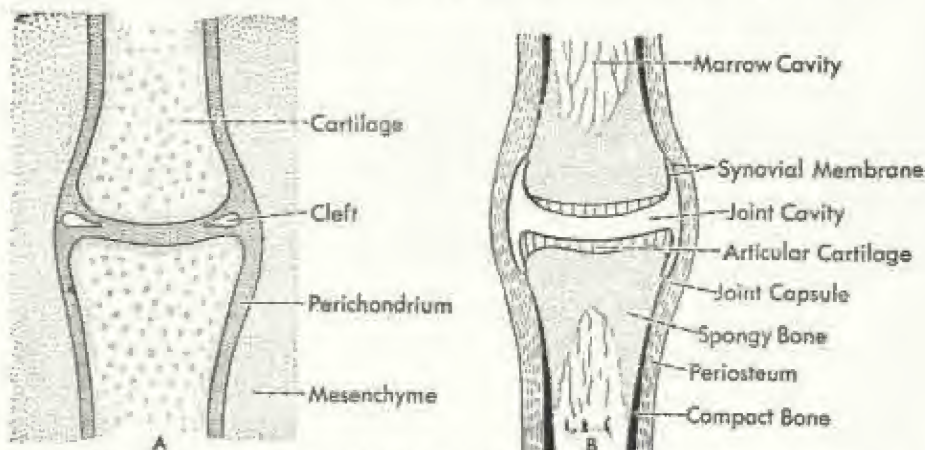


Fig. 424. A freely movable joint (diarthrosis). A, developmental stage; B, completed joint. (After Arey.)

A typical joint, however, is one which allows freedom of motion between the bony partners, and by means of skeletal levers makes locomotion possible. These freely movable joints (*diarthroses*) include *hinge joints*, as at the elbow and the knee, and *ball-and-socket joints* which occur at the shoulder and the hip.

A diagram of such a movable joint (Fig. 424) shows that the two neighboring bones do not come into direct contact with each other, but instead their frictional surfaces are faced with yielding cartilage. Between these cartilage surfaces there is inserted a closed sac, or *bursa*, filled with a lubricating *synovial fluid* continuously secreted by the cells lining the sac. Outside of these skeletal elements a fibrous air-tight sheath holds the bones together by atmospheric pressure without muscular effort. In mountain climbing a familiar experience is a sense of heaviness at the joints, resulting from the change in atmospheric pressure.

Outside of the joint there is an equipment of muscles controlled by directive nerves. Thus the operation of movable joints involves the combined action of bone, cartilage, connective tissue, muscle, and nerve.

III. DIVISIONS OF THE SKELETON

The hard skeletal parts are usually grouped into the *axial* and the *appendicular* divisions of the skeleton. The axial skeleton includes the skull, vertebral column, ribs, and sternum, while the appendicular is composed of the pectoral and pelvic girdles as well as the skeleton of the appendages.

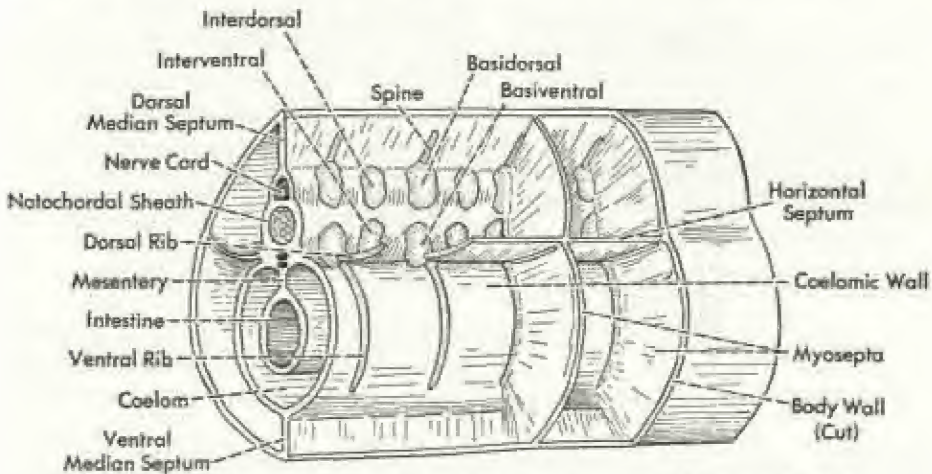


Fig. 425. Diagram of the connective tissue system of the trunk of a vertebrate, showing relation of axial skeleton to transverse and longitudinal septa. Oblique view of left side. (After Goodrich.)

As described in Chapter VII, the cartilaginous and bony elements are laid down first as connective tissue. During embryonic development, connective tissue derivatives of the mesenchyme become widely distributed throughout the body, contributing to the body wall, the various organs, and

the linings of body cavities, as well as filling in around the myotomes and grouping about the notochord and embryonic neural tube (Fig. 425). A median *dorsal septum*, separating the dorsal parts of the myotomes of the two sides of the body, extends from the region of the neural tube to the mid-dorsal line, while the ventral ends of the myotomes are separated by a *ventral septum*. Between successive myotomes are transverse *myocommata* which are continuous with the median septa and also with a *horizontal septum* which splits each myotome into a dorsal and a ventral part.

IV. THE MAIN SKELETAL AXIS

Vertebrates are bilaterally symmetrical animals with the long dimension of the body stiffened by a *skeletal axis*, usually in the form of a backbone lying between two tubes that also run lengthwise the body.

The *digestive tube* lies below the axis. It is ordinarily much longer than the body itself, and consequently is more or less coiled. The *neural tube* extends just above the axis and is relatively short and straight like the backbone which encases it. Thus, the skeletal axis is in intimate and fundamental relations with both the main nervous and the digestive systems, having evolved primarily to meet the mechanical necessities arising from a locomotor bilateral type of symmetry.

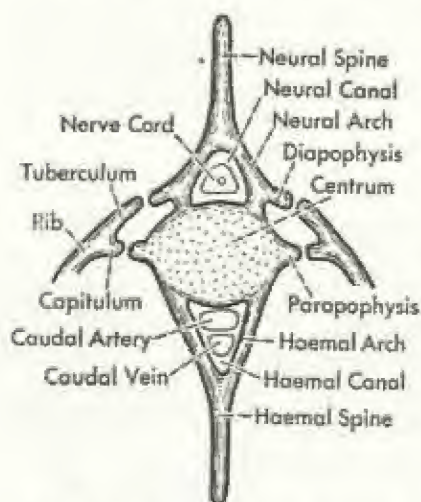


Fig. 426. A generalized vertebra.

lend the entire backbone a certain degree of flexibility without sacrificing the stiffening quality for which the "backbone" stands.

Most vertebrae consist of a main body, or *centrum*, bearing one or two arches and one or more pairs of processes (Fig. 426). The centrum first appears as a ring of tissue which develops around the notochord and then fills in to become a disc or cylindrical mass. Fused with the dorsal side of the centrum is a *neural arch* enclosing a *neural canal* through which the delicate spinal cord safely threads its way. Usually a *neural spine* extends

1. The Parts of a Vertebra

The skeletal axis is for the most part composed of separate bony elements, or *vertebrae*, of which there are 32 or 33 in man, so fashioned as to

from the mid-dorsal part of the arch into the dorsal septum. In the caudal region of many vertebrates there is, in addition, a similar set of structures on the ventral side of each vertebra. They are called *haemal arch*, *haemal canal*, and *haemal spine* because through the canal run the caudal artery and vein (*haema*, blood).

Projecting in various directions from the centrum and the base of the neural arch are several outgrowths, or *processes*, which offer convenient surfaces either for the attachment of muscles, or for frictional contact of one vertebra upon another in a sliding joint. On the arch are *zygapophyses* (*zyg*, yoke, joined; *apophysís*, process) so called because they bear the surfaces for articulation between vertebrae. There are usually two pairs of these processes, anteriorly projecting *prezygapophyses* and posteriorly projecting *postzygapophyses*. The articular surfaces are on the dorsal sides of the anterior processes and on the ventral sides of the posterior ones (Fig. 427). The arrangement of the articular surfaces is "onward and upward," that is, the "onward" or anterior process has its articular surface on the "upward" or dorsal side. Thus it is possible to determine the anterior face of an isolated vertebra.

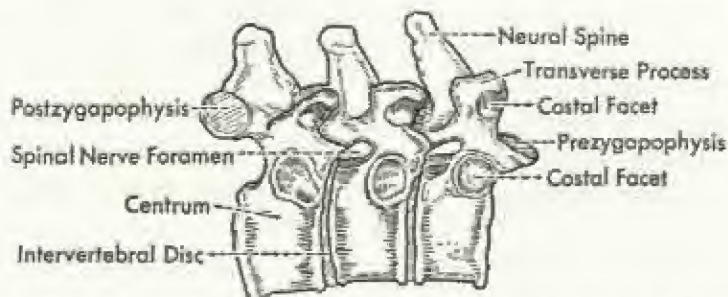


Fig. 427. The tenth, eleventh, and twelfth thoracic vertebrae shown from the right side.

Extending laterally from the sides of the vertebra are *transverse processes* which are primarily associated with the ribs. Originally on the arch, but occasionally shifting over onto the centrum, is a pair of laterally projecting *diapophyses* which articulate with the dorsal heads of Y-shaped, dorsal ribs. On the centrum is another pair of these transverse processes, the *parapophyses*, which articulate with the ventral heads of these Y-shaped ribs. Frequently one or the other of these pairs of transverse processes is weakly developed or absent.

Movement of skeletal parts depends upon the presence of joints with

their equipment of muscles, blood vessels, and nerves. In those regions of the backbone, therefore, where movement is most needed, as for instance in the neck, the various articular processes of the vertebrae are found to be most elaborated. Where rigidity and a minimum, or the entire absence, of movement between the vertebrae is desirable, as for example in the sacral region, all processes are much reduced.

The parts which constitute a typical vertebra undergo the widest variation, not only in the different species of vertebrates but even in the different vertebrae making up the backbone of any individual.

Vertebrae form the chief mark that brands an animal as a vertebrate, and the phylogeny of these structures has never been successfully traced back to any invertebrate source. Such a new structural invention that has not been led up to by a series of gradual modifications in ancestral forms the biologist hails as a *neomorph*.

Within the vertebrate class the steps by which the vertebrae have taken form have been traced in considerable detail, both by the embryologist and by the palaeontologist.

2. The Notochord and Its Sheaths

The embryonic formation of the vertebrae is preceded in every backboned animal by a temporary skeletal axis called the *notochord*. The position of this temporary axis, which lies lengthwise between the neural cord and the digestive tube, is the same as that of the centra of the vertebrae which replace it later.

Differing from other skeletal tissue such as bone and cartilage in which intercellular material may be excessively developed, the cells of the notochord are at first large, thin-walled, and closely packed together. They are enclosed in a thin tough sheath of connective tissue, the *elastica externa*, mesenchymal in origin. Notochordal cells are devoid of both nerve supply and blood vessels. They are, therefore, nourished vicariously by diffusion from outside cells.

As the notochord grows older the cells within the sheath change. The marginal ones next the primary sheath itself form a definite layer of *peripheral notochordal cells* (Fig. 98), while those in the central part tend to become vacuolated, losing their outlines and fusing together. The peripheral cells are then transformed into a thick, fibrous *secondary sheath* inside of the primary one, with the result that the notochord as a whole at this stage might be described as a somewhat rigid cylinder tapering at either end, made up of the remains of closely packed turgid tissue surrounded by a dense double sheath.

In amphioxus, cyclostomes, dipnoans, and certain other fishes, the vertebral column evolves no further than the notochordal stage, except for the presence in some instances of vertebral arch elements laced by connective tissue to the notochord. In other vertebrates, after the notochordal stage is passed, an axial skeleton of another and more complicated sort is established upon its ruins. The notochord, therefore, is the oldest part of the vertebrate skeleton, antedating cartilage and bone not only during the development of the individual but also in the long phylogeny of vertebrate types.

3. The Formation of Vertebral Arches

Although *support*, in the form of a stiff rod through the long dimension of the bilaterally symmetrical animal, is the earliest function that any skeletal tissue performs in a vertebrate, the supplementary function of *protection*, particularly of the precious nerve cord lying just above the notochord, begins to become manifest very early.



Fig. 428. Diagram of a piece of the notochord of a lamprey eel, with cartilaginous arches (paired rods) saddled upon it. These are the beginnings of neural arches. Position of nerve cord indicated by the arrow.



Fig. 429. Ball-and-socket vertebrae of an adult alligator, showing the suture between the centrum and the neural arch still persisting.

Along the notochord and on either side of the nerve cord of the primitive lamprey eel, *Petromyzon*, pairs of small cartilage struts appear, distinctly foreshadowing the future neural arches of the higher vertebrate types (Fig. 428). At first these pairs of strutlike plates do not meet and fuse together to form complete arches, but in later evolutionary stages this does happen, usually through the insertion of a keystone of cartilage or bone that becomes the dorsal *neural spine* (Fig. 426).

The original independence of the neural arch from the centrum is demonstrated not only by the fact that these two parts develop separately but also for the reason that in young mammals, as well as in adult alligators and turtles, distinct sutures may be seen between arch and centrum

(Fig. 429). The same general story is told upside down by the haemal arches (Fig. 426).

4. The Embryonic Development of Vertebrae

During the consideration of vertebrate development it was noted that segmentally arranged sclerotomes are formed from mesenchyme given off by the medial sides of the epimeres. These sclerotomes are arranged as two rows of blocks, one row running along each side of the notochord (Fig. 430). Each sclerotome differentiates into a more compact posterior half and

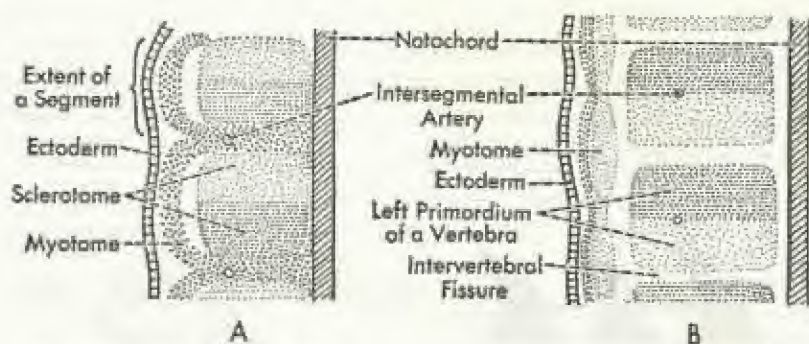


Fig. 430. Diagrammatic frontal sections at level of notochord, showing differentiation of sclerotomes of left side only. Each sclerotome differentiates into a less compact anterior part and a more compact posterior part, as shown in A. After the two halves have separated, the posterior half of each sclerotome fuses with the anterior half of the sclerotome next behind it to form a primordium of a vertebra, as in B. Each vertebra develops from a pair (right and left) of such primordia. (After Arey.)

a less compact anterior half. Ultimately the two parts separate and the posterior half of one sclerotome joins with the anterior half of the next sclerotome to form a vertebra. In this manner each vertebra comes to occupy an intersegmental position with the myotome attached to the middle of the centrum. As the myotomes retain their original segmental positions, each becomes associated with two vertebrae. This relationship is a necessity if the myotomes are to bend the vertebral column.

Two centers of chondrification (cartilage formation) appear in each half-sclerotome. One of these is just above the notochord, the other just below. The cartilages and associated mesenchyme cells of the more compact posterior half-sclerotome are known as *basals*, a dorsal *basidorsal* and a ventral *basiventral* (Fig. 431). The corresponding regions of the anterior half-sclerotome, or the *interbasals*, are an *interdorsal* and an *interventral*.

Thus there are four regions, known as *arcualia*, in each sclerotome (four pairs in each segment).

The four pairs of arcualia may spread and fuse in various ways within different types of vertebrates. Some of them may even vanish entirely in the course of the subsequent formation of the vertebrae. In most vertebrates the basidorsals grow upward to form the neural arch while the basiventrals grow downward to form the haemal arch. The development of the centrum region varies greatly in different vertebrate groups.

In cartilaginous fishes the centrum is formed largely by cells from the two pairs of basal arcualia (basidorsals and basiventrals) which break through the *elastica externa*. Within the fibrous secondary sheath they form a ring of tissue which soon begins to chondrify. The cartilaginous ring, the beginning of the definitive centrum, continues to grow by the addition of new material onto its anterior and posterior surfaces and by filling in toward the center. This centripetal growth slowly constricts and squeezes out the enclosed notochord. Ultimately, in the adult, the circular band of cartilage

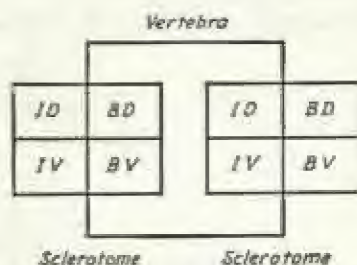


Fig. 431. The basidorsals (bd) and the basiventrals (bv), are responsible for the anterior half of the vertebra, while the interosseous (io) and the intervertebrals (iv) account for the posterior half.

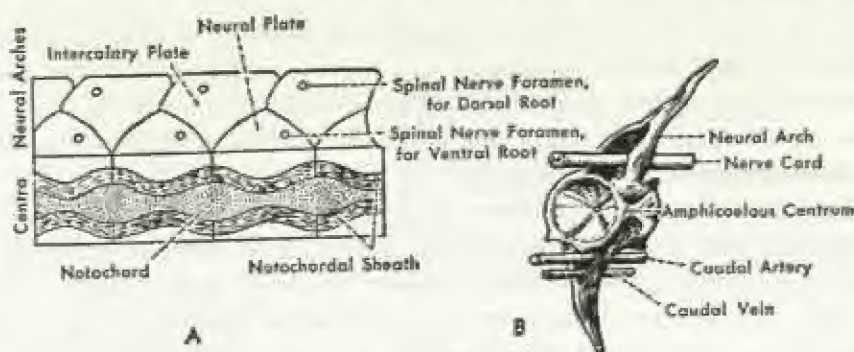


Fig. 432. The vertebral column of fishes. A, sagittal section through vertebral column of a shark; B, caudal vertebra of a bony fish, showing nerve cord and blood vessels which run through it. (B, after Jammes.)

is thickest in the mid-part of the vertebra so that the notochord is nearly eliminated at that point but only slightly constricted at the intervertebral level (Fig. 432A). The cartilaginous centrum as a whole, therefore, has a concavity on each end occupied by notochordal tissue. Such a biconcave

centrum is said to be *amphicoelous* (*amphi*, both; *coel*, cavity). These centra, which develop within the tissue of the notochord, are known as *chordal centra* in contrast with the *perichordal centra* of bony fishes and tetrapods which develop from mesenchyme remaining outside the *elastica externa*. Even in the cartilaginous fishes some perichordal cartilage is eventually added to the original chordal centrum.

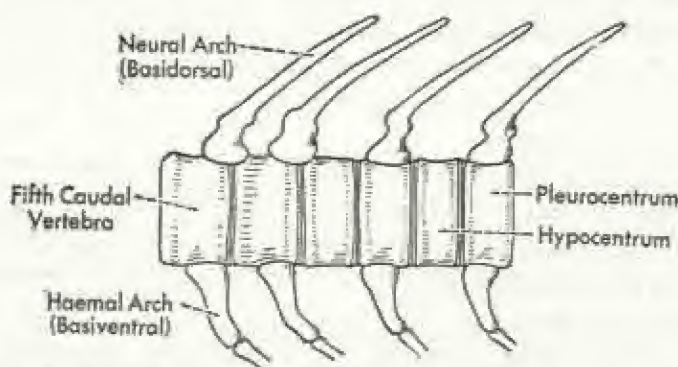


Fig. 433. Caudal vertebrae of *Amia calva*, left side view. (After Goodrich.)

In the bony fishes the perichordal centra are usually laid down directly as bone without any intermediate cartilaginous stage as in tetrapods. Perhaps the most interesting feature of the vertebral column of these animals, however, is the occurrence of two centra per segment in most of the tail region of *Amia* and a number of other genera (Fig. 433). The more anterior of the central discs, or the *hypocentrum*, is formed in part at least from an enlarged basiventral while the more posterior *pleurocentrum* owes its development to the interdorsal.

Apparently the most primitive of the amphibians, some of the stegocephalians, had both hypocentral and pleurocentral elements throughout the entire length of the vertebral column. From the plan found in these animals there seem to have been two evolutionary lines, one in which the hypocentrum is emphasized, the other the pleurocentrum. In modern amphibians the centrum is largely a hypocentrum, while in amniotes it is mainly a pleurocentrum (Fig. 434).

The mammalian vertebra, therefore, develops from three of the four pairs of arcualia. Neural and haemal arches arise from basidorsals and basi-ventrals, respectively, of one pair of sclerotomes, while the centrum is largely a derivative of the interdorsals of the next pair, the intervertebrals of which disappear (Fig. 431). Between the bony centra are *intervertebral*

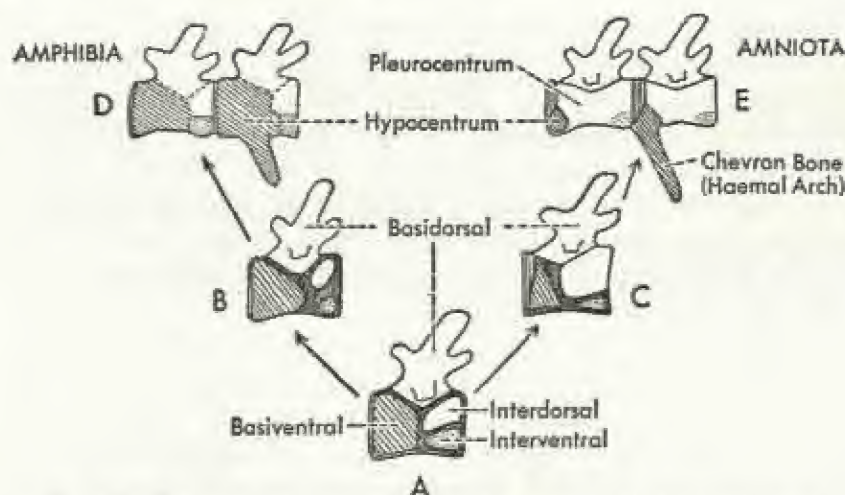


Fig. 434. Diagram illustrating supposed divergence in development of vertebral elements leading from a primitive ancestral tetrapod (A) to a typical amphibian (B) and a typical amniote (E). A caudal vertebra is added in B and E. (After Goodrich.)

discs of fibrous cartilage formed from basiventrals which are not otherwise utilized throughout most of the trunk region. In the core of each of these discs, even in adults, may be found a persisting notochordal remnant called the *nucleus pulposus* (Fig. 435). If this "nucleus" could indulge in reminiscence what a story of evolution it could tell!

The vertebrae of mammals differ from those of all other vertebrates in having epiphyses which develop as separate intervertebral bony discs one at each end of each centrum. Some time after birth they usually fuse with the main central mass.

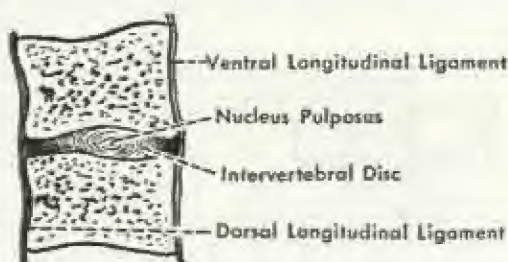


Fig. 435. A long section through the centra of two vertebrae and an intervertebral disc in the center of which the last remains of the notochord show as the *nucleus pulposus*. (After Gegenbaur.)

5. Types of Articulation between Centra

All vertebrae articulate end to end. But the ends of vertebrae vary in shape. Hence the type of joint between vertebral centra differs in the various classes and, in some cases, even in different regions of the same animal. The five commonest types of articulation are: (1) amphicoelous; (2) procoelous; (3) opisthocelous; (4) heterocoelous; and (5) amphiplatyan.

The amphicoelous type is found in most fishes, in primitive amphibians (stegocephalians) and primitive reptiles (cotylosaurs) as well as some living amphibians (e.g., *Proteus* and *Necturus*) and reptiles (*Sphenodon*, some lizards and, to a certain extent, turtles). As mentioned previously the centrum of such a vertebra is concave at both ends (Fig. 432). Owing to the fact that the actual contact is limited to the edges of the two cups, placed rim to rim, little freedom of movement is possible between the vertebrae held in place by considerable connective tissue, hence the limitation of this type mainly to water-dwellers.

In a procoelous vertebra the cavity on the anterior end (*pro*, before) is retained but the posterior end fills in and becomes convex (Fig. 429). There is, therefore, a simple type of ball-and-socket joint which allows considerable movement because of the reduced amount of connective tissue needed to lace together the vertebrae. Procoelous vertebrae occur in some anurans, chiefly frogs and toads, in the extinct pterosaurs, and in modern reptiles, including Lacertilia, Ophidia, and Crocodilia. The somewhat rare condition of a biconvex vertebra is found in the case of the sacral region of *Bufo* and *Rana* and the first tail-vertebra of Crocodilia.

The opisthocoelous condition, the reverse of the procoelous, has the concavity on the posterior end (*opisthos*, behind). These vertebrae are not characteristic of any major group but are found in widely separated species or Orders among all vertebrate Classes except cyclostomes. Examples are:

Lepidosteus, the exception to the amphicoelous condition typical of fishes; some anurans; dinosaurs (cervical vertebrae only); penguins, parrots, and a few other carinate birds; and ungulate mammals (cervical only).



Fig. 436. Ventral view of one cervical vertebra of a swan, and a part of another, showing a saddle joint, the movement of which is not only in the direction of the arrows but also at right angles to them. Anterior is toward the left.

Heterocoelous vertebrae are the usual type in birds, especially in the cervical region (Fig. 436). These are also known as saddle-joint vertebrae because of the somewhat remote resemblance of the articulation to the situation of a rider in a saddle. The anterior end of the centrum is rounded off dorso-ventrally so that it appears convex in a section through it in the sagittal plane. Short processes extend anteriorly from the lateral parts of the

centrum to give it a concave appearance in frontal sections. At the posterior end this condition is reversed. The elevations, on the dorsal and ventral parts of the centrum in this region, fit over the rounded part of the anterior end of the next centrum, while the rounded region of the posterior end fits

between the elevations on the sides of the anterior end. Great freedom of movement between these vertebrae is permitted.

Amphiplatyan vertebrae (Fig. 427), flat on both ends (*amphi*, both; *platy*, flat), are typical of mammals.

6. History of the Vertebral Column

The total number of vertebrae in the backbone of an animal does not ordinarily increase with age and growth. On the contrary, as the result of fusion, the number frequently decreases in adult life. Frass reports that the tail vertebrae of one species of fossil ichthyosaurs varied from 129 to 160 according to the size and probable age of the specimen examined. There are usually more vertebrae in the lower fishes than in higher forms, and in general deep-sea fishes have a larger number than those inhabiting shallow waters. David Starr Jordan cites the curious fact that certain kinds of fishes living in the southern part of their range have more vertebrae than representatives of the same species in more northern waters.

Of all vertebrates pythons probably hold the record for the largest number of vertebrae, one having been reported with as many as 435.

While the vertebrae composing the backbone are easily referable to one structural plan, no two are exactly alike. The variations that have arisen are closely correlated with the diverse kinds of work which each vertebra, or group of vertebrae, has to do. Since it is desirable, for example, to have the head move in any direction without turning the entire body, the vertebrae of the neck which carry the head have developed joints that permit freer movement than is found elsewhere along the skeletal axis. The sacral vertebrae, on the contrary, whose function, particularly in bipedal animals, is to bear the weight of the body upon the legs, have entirely lost their movable joints and become fused together into a solid efficient unit of support (Fig. 437).

The point of attachment for the legs, as well as the region where the ribs are present, serve as landmarks, dividing the vertebral column of man and the higher animals into five natural groups of vertebrae, namely, cervical, thoracic, lumbar, sacral, and caudal.

The forerunner of the vertebral column is the notochord. The only part of the axial skeleton present in lowest chordates, it persists as a well developed

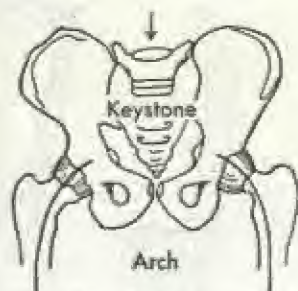


Fig. 437. A diagram showing the part the fused sacral vertebrae play as a keystone of the arch that supports the weight of the body.

unconstricted structure in cyclostomes, dipnoans, cartilaginous ganoids, and a few other fishes in which no central rings develop about it.

Among the cyclostomes only the lamprey eels have vertebral elements. Throughout most of the trunk region each segment has two pairs of cartilaginous rods attached to the notochordal sheath and extending dorsally alongside the nerve cord (Fig. 428). These elements are probably the homologues of basidorsals and interdorsals. As the rods do not meet dorsal to the nerve cord, the neural canal is roofed over by connective tissue. In the posterior trunk region these structures become reduced and irregular. The absence of these parts in hagfishes is believed to be due to degeneration.

Among fishes the vertebrae posterior to the anal region develop haemal arches on the ventral side of the centra (Fig. 432a). The spinal column, therefore, may be divided into *trunk vertebrae*, essentially alike, which are anterior to the anus, and postanal *caudal vertebrae*, possessing the haemal arch and diminishing progressively in size toward the posterior end.

A slightly modified condition exists in the amphibians, with a smaller total number of vertebrae involved. A single cervical vertebra, providing for the beginnings of independent head movements, is inserted next to the skull, while between the trunk and caudal vertebrae there is differentiated a single

sacral vertebra (lacking in the limbless apodans) to which the hind legs are attached. The anchorage of the hind legs to this solitary inadequate sacral vertebra is one of the reasons why the amphibians are unable to "stand up" and bear their weight upon their hind legs. Amphibians are the first vertebrates with well developed zygapophyses.

In adult frogs the caudal vertebrae are fused together into a long *urostyle* (Fig. 438), which acts as a counterpoise for the teetering body that is swung in the crotch formed by the pelvic girdle. Any jumping animal like a

frog needs a shock-absorbing device much more than a creeping or walking animal does, in order to lessen the jar that is communicated to the brain when it lands. This is nicely provided for in the frog by the way in which the unsteady body is swung in the remarkable, iliac crotch of the pelvic girdle, and at the same time is prevented from jack-knifing together by the counter-

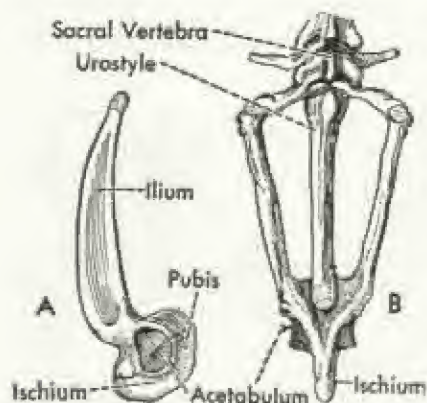


Fig. 438. Pelvic girdle of a frog, *Rana*. A, lateral view of right half; B, dorsal view to which are added vertebral elements.

poising urostyle and the muscles that hold it in place. The frog may not have much of a brain but that is all the more occasion for taking care of what there is of it and not shaking it up unnecessarily.

Among reptiles the differentiation of the vertebrae includes several advances. With the exception of snakes and footless lizards, living reptiles are characterized by having *two sacral vertebrae* for the attachment of the pelvic girdle and the support of the hind legs, while the trunk vertebrae usually become specialized at either end into *cervical* and *lumbar* vertebrae respectively, between which are the rib-bearing *thoracic* vertebrae. The lumbar vertebrae, being free from complications of ribs, permit a certain amount of twisting in the lumbar region of the vertebral column. This is more pronounced in agile carnivores than in less active herbivores. Not all reptiles, however, are equally diversified with regard to vertebrae. In snakes, for example, there is little differentiation of the column, all vertebrae being much alike and bearing paired ribs. In turtles only the cervical and caudal regions are flexible. The trunk, not differentiated into thoracics and lumbar, and sacral regions are immovably fused with plates along the center of the dorsal shell, or *carapace* (Fig. 439).

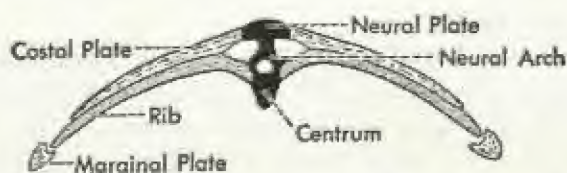


Fig. 439. Cross section through the carapace of a turtle. (After Huxley.)

The vertebrae of birds undergo great modification in connection with adaptation to flight. The cervical vertebrae undergo much differentiation, reaching the maximum number for any vertebrate. A flexible neck is a prime necessity for a bird which, lacking hands, must pick up all its food either with a prehensile beak or with the talons of its claws. Even an owl can turn its staring eyes in any direction because its apparently very short neck has so many joints. This cervical flexibility is also of importance because the thoracic vertebrae are more or less fused together. This condition, with accompanying modifications of the ribs and sternum, furnishes a stable attachment for the muscles of flight while at the same time keeping the weight of these structures at a minimum. Similarly, firm support for the legs is provided by fusion of the posterior thoracic, all lumbar, the two sacral, and the anterior caudal vertebrae into a single *synsacrum* to which the pelvic girdle is attached. As many as 23 vertebrae may contribute to the

synsacrum. Beyond this region there are several separate caudal vertebrae followed usually by a *pygostyle* formed by the fusion of the last few caudals.

In mammals the cervical vertebrae typically number seven, whether the neck is functionally absent, as in the whales where the cervical vertebrae are all fused together, or conspicuously present, as in the bizarre, long-necked giraffes.

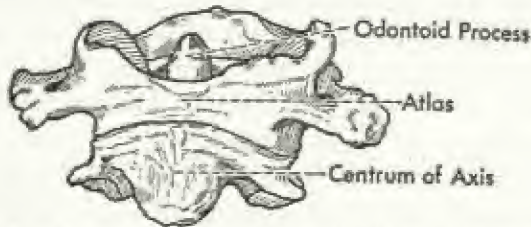


Fig. 440. The human atlas and axis, ventral view. (After Sobotta and McMurrich.)

There are four known exceptions to this rule of seven: the three-toed sloth, *Bradypus*, has nine cervical vertebrae; the ant-bear, *Tamandua*, eight; while the two-toed sloth, *Choloepus*, and the American sea cow, *Trichechus*, each has six.

As in reptiles and birds, the first two cervical vertebrae of mammals are further specialized into the so-called *atlas* and the *axis* (Fig. 440). The atlas, according to Vesalius, takes its name from human anatomy, since in man it "bears the weight of the world" upon its shoulders in the form of the head,

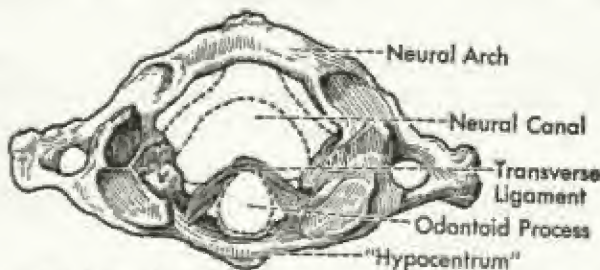


Fig. 441. Relation of odontoid process to atlas in man, as seen from the anterior (superior, of human anatomical terminology) side. (After Gray.)

after the fashion of its classical prototype. Two articular surfaces at the base of the skull in mammals, the *occipital condyles*, are in frictional contact with two corresponding surfaces on the atlas, thus forming a joint that allows for the nodding movements of the head. The atlas is virtually without the

projecting neural spine of a typical vertebra, and, unlike the first vertebra of fishes and amphibians, has no centrum. The embryonic centrum of the atlas (interdorsal of the second trunk sclerotome) fuses onto the anterior end of the centrum of the axis, or second cervical vertebra, to form a large projection, the *odontoid process*, which extends forward toward the skull



Fig. 442. A profile showing the *vertebra prominens*.

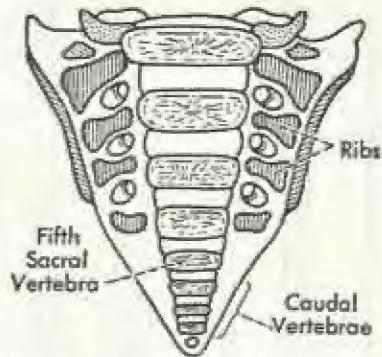


Fig. 443. Sacrum of a human fetus five months old, showing sacral ribs. (After Köllmann.)

and rests on the floor of the atlas ring (Fig. 441). As a result the axis is really outfitted with two centra. The atlas would be open ventrally were it not for the fact that basiventral material, which ordinarily forms only intervertebral discs in the trunk region, is added to the other parts of the vertebra to form a complete bony ring.

The articulation between the skull and the atlas is the "yes" joint permitting human beings to nod approval, while the atlas-axis articulation is the "no" joint by means of which disapproval is indicated by shaking the head sidewise. The graceful up and down movements of the head of a playful dolphin involve the whole plunging body as well, for these stiff-necked creatures are unable to say "yes" in the orthodox cervical fashion. Modified cervical vertebrae occur also in the burrowing moles, which have the second, third, and fourth cervicals fused solidly together, to the decided advantage of these subterranean tunneling engineers.



Fig. 444. The human coccyx.

The neural spines of the cervical vertebrae in man are frequently more or less forked, a modification more apparent in modern civilized races than among either primitive races or man's apelike cousins. The seventh cervical vertebra has the longest neural spine, notably so in females. It is unforked and projects backward, forming a protuberance under the skin at the base of

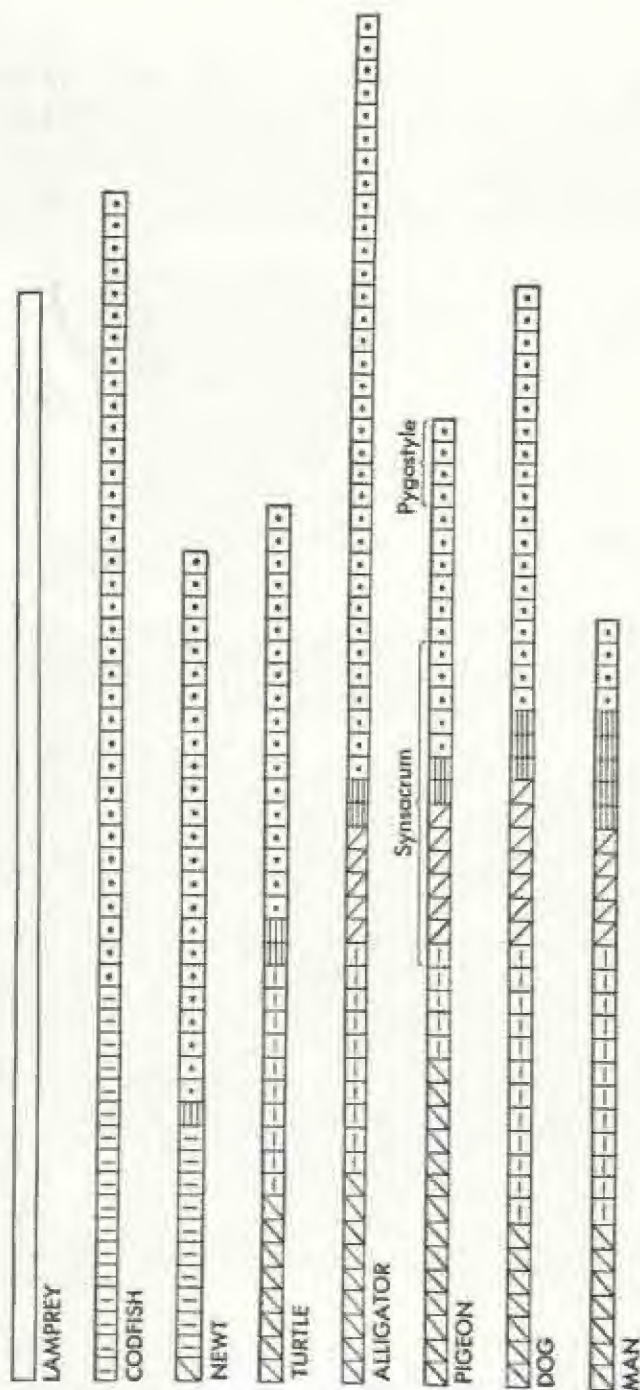


Fig. 415.

Diagram of the differentiation of the vertebrae in representative vertebrates.

the neck when the head is bowed forward. For this reason it is called the *vertebra prominens* (Fig. 442).

In the human embryo there are present seven cervical, twelve thoracic, five lumbar, five sacral, and four, five, or sometimes as many as eight caudal vertebrae. In the adult the five sacral vertebrae, together with the embryonic sacral ribs, fuse to form a single *sacrum* (Fig. 443). Usually all the caudal vertebrae are joined together to make the *coccyx*, although it is not very exceptional for one or two of the most posterior caudal vertebrae to retain their independence (Fig. 444). Rarely the occurrence of tails several inches in length, containing degenerate caudal vertebrae, have been authentically reported in adult human beings.

The differentiation of vertebrae in the vertebrate series is visualized diagrammatically in Figure 445.

7. The Entire Backbone

The units of the vertebral column when taken together are more differentiated at either end than in the middle. In the higher vertebrates particularly notable specialization of the cervical vertebrae is connected with head movement, while the frequent pronounced degeneration of the caudal vertebrae is apparently an expression of disuse.

The backbone taken as a whole has in general three uses, namely, support, protection of the nerve cord, and movement.

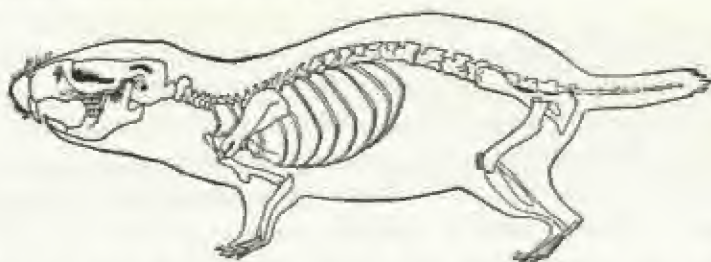


Fig. 446. Skeleton of a rodent with its arched vertebral column from which various parts are suspended.

The *function of support* is what may be called the "backbone" function proper. The solid bony axis is arranged lengthwise the body because in this way the greatest number of parts can be conveniently accommodated with a sustaining anchorage. In tetrapods particularly the spine is an arch from which a variety of things are suspended (Fig. 446), whereas in bipedal animals like man, that tip up on end and poise a heavy head on top of the vertebral column, the function of support is more effectually accomplished because of certain adaptive curvatures in the backbone which make the

column mechanically more capable of sustaining weight and at the same time more flexible. The human vertebral column has four dorso-ventral *curvatures*, namely (1) the *cervical*, concave dorsally; (2) the *thoracic*, concave ventrally; (3) the *lumbar*, concave dorsally and forming a long sweeping arch; and (4) the *sacral*, concave ventrally (Fig. 447). The lumbar curvature does not occur in other mammals. These curvatures, which are due more to modifications of the padlike fibrous cartilages be-



Adult Infant

Fig. 447. Diagrams showing the difference in the curvature of the backbone between an infant and an adult.

tween the separate vertebrae than to any modification in the shape of the centra that are stacked one upon the other, are less pronounced in infants and in primitive races than in adult civilized man. The human cervical curvature usually develops when the child begins to sit up while the lumbar appears when the child starts walking. The delayed appearance of the lumbar curvature, that gives the typical hollow back to a well-formed man, is particularly noticeable. Babies which lack it are flat-backed, like their remote quadrupedal ancestors, and are consequently awkward and uncertain on their feet.

A second function of the backbone as a unit is the *protection of the nerve cord*, which is an indispensable cable of great complexity, extremely delicate and liable to injury. It is not only ensheathed in its own envelopes, or *meninges*, but it is also surrounded by protective jackets of fluid and is furthermore encased within a bony conduit formed by the neural arches of the vertebrae. Between the neural arches are *spinal nerve foramina*, passageways for these nerves (Fig. 427). Even the backbone itself is overlaid with ligaments and buried with its valuable contents so that it is still further protected from outside injury by surrounding muscles and fatty tissues. Finally the whole internal mechanism is effectually sealed up within the tough, resistant, practically germ-proof skin.

The third general function of the spinal column is *movement*, and while this is relatively slight between any two vertebrae, when taken all together it amounts to enough to be noticeably missed by anyone afflicted with a stiff neck or a lame back. There are said to be over 150 different articular surfaces along the length of the human backbone, which explains the reason why professional contortionists, and babies whose vertebrae are still in the making, are able to demonstrate so amazingly the possible flexibility of the vertebral column.

The pliability of the backbone is largely due to the springy compressible intervertebral discs which make up approximately one fourth of the entire length of the vertebral column. These discs are buffers, like the bumpers between the cars of a railroad train that take up the shock of impact. Without them the jolting effort of locomotion would affect the central nervous system quite like riding in a springless ox-cart instead of in a luxurious automobile. A traffic policeman who has been on his feet all day is a measurable bit shorter at night than in the morning because of the packing down of the compressible intervertebral discs of his spinal column. In old age these discs lose much of their elasticity and in second childhood it is no longer feasible to try to imitate a baby that delights in inserting its toes in its mouth.

Movement of the spine in turtles is confined to the flexible cervical and caudal regions, but in snakes it is uniformly possible along the entire length of the body, although the vertebrae are so firmly interlaced and held together by ligaments and muscles that these sinuous animals are unable to make abrupt angular bends.

The caudal part of the backbone exhibits a great variety of movements peculiar to different vertebrates and often quite unlike the movements of the rest of the backbone. Such movements serve a wide range of uses, for example, sculling locomotion in fishes, prehension in long-tailed monkeys, removal of annoying insects in cows and horses, and expression of the emotions in dogs.

Some lizards have a peculiar breaking-plane within the centra of many of the caudal vertebrae that enables them in an emergency to snap the tail off when harassed by a pursuing enemy. The part of the tail thus sacrificed continues for some time to jerk and bob about, thus tending to divert the attention of the pursuer, permitting the persecuted bob-tailed lizard to escape and grow a new tail in safety.

V. THE THORACIC BASKET

I. In General

The vertebral column, as already pointed out, has to do with the tubular dorsal nerve cord. The other one of the two essential tubes that characterize the vertebrate body, namely, the digestive tube, is encircled and protected at least partially by another part of the skeleton, the *thoracic basket* (Fig. 297). This consists primarily of the thoracic vertebrae, the ribs, and the breastbone, with the pectoral girdle sometimes playing a supplementary rôle.

Since the digestive tube in most instances is many times longer than the body, it is coiled up in a compact mass that requires a "basket" for its

skeletal protection instead of a straight narrow sheath such as is adequate for the nerve cord.

The thoracic basket first comes into its own with life on land in the class Reptilia, where a true breastbone and encircling ribs are present. This combination of bones and cartilages, which is hung on the anterior part of the

skeletal axis, not only encloses a considerable portion of the digestive organs, but also furnishes protection to other soft viscera, notably the heart and lungs that are in great need of skeletal protection. In higher vertebrates still other organs, originally contained within the thoracic basket, have lost this protection, either by the contraction or degeneration of the structure itself, thus exposing the parts formerly protected, or by shifting their position. Liver, spleen, pancreas, and the small intestine, much of which is exposed, receive only partial protection from the thoracic basket, while the kidneys and gonads have migrated far posteriorly from their embryonic or ancestral position within the basket.

The thoracic basket in man is marked off at either end by more or less transverse areas, while the sides are made up of skeletal elements embedded in muscular walls. The top of the basket is a somewhat restricted region, the margin of which is determined by the first thoracic vertebra, the first pair of ribs, and the upper end of the breastbone (Fig. 448). This enclosed space marks a narrow passage-way through which there are crowded side by side various structures, providing for traffic between the head and trunk (Fig. 449). There is first the

trachea, connecting the imprisoned lungs with

the outside world; next, the *esophagus*, that passes along food and drink, placing it safely beyond normal recall; the *vagus nerves*, wandering far from their headquarters in the brain to supply the distant viscera below; the large *carotid arteries* and *jugular veins*, which collect and distribute the blood of the head; and finally, a loop of the *thoracic duct*, that brings back into the confines of the venous system escaped white blood cells from their peregrinations throughout the tissues of the body.

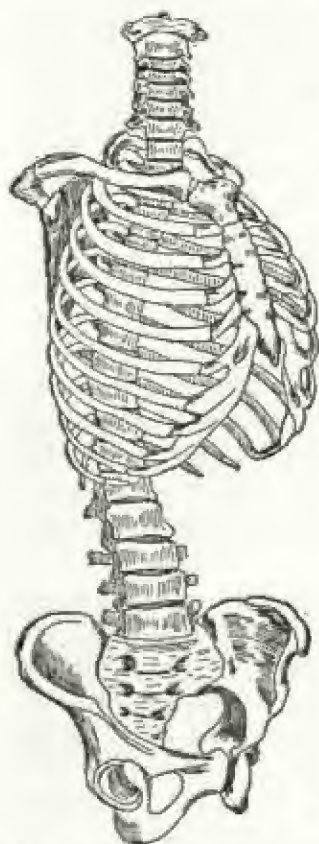


Fig. 448. The backbone, thoracic basket, and girdles. (After Bell.)

The floor of the basket, which in man is larger than the top area, is bounded behind by the last thoracic vertebra together with the short twelfth pair of floating ribs attached thereto. On the sides and in front the margins of the floor are determined by the tips of the tenth and eleventh pairs of ribs and by the cartilages of other posterior ribs that attach the latter to the breastbone, as well as by the lower end of the breastbone itself. The floor is also closed crosswise by the vaulted diaphragm which separates the cavities containing the lungs and heart above from the abdominal cavity below. This partition, or floor, of the thoracic basket tends to slope backward from the sternum towards the backbone, while the slant of the margin around the space marking the smaller top of the basket slopes upward from the sternum towards the backbone, since the sternal length is shorter than the vertebral length.

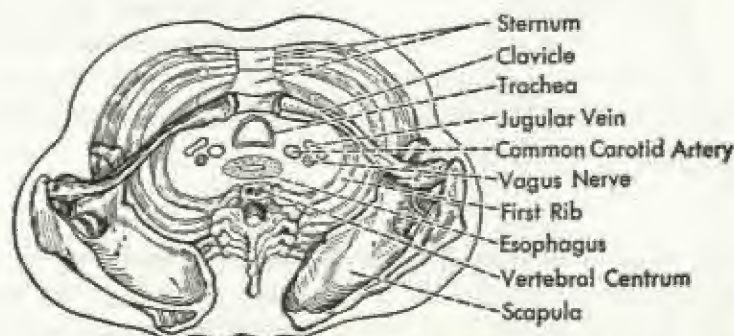


Fig. 449. Diagram of the anterior opening of the thoracic basket as seen from above. (After Witkowski.)

In general, therefore, the contour of the whole basket is somewhat cone-shaped with the smaller, upper end towards the head.

The space within the thoracic basket is partially divided into right and left spaces bulging dorsally like bay windows from the general cavity, since the upright column formed by the centra of the vertebrae, stacked one upon the other, stands out into the cavity, thus serving to a certain degree as a longitudinal partition. Within these lateral enlargements are packed the lungs. The heart lies midway between the lungs instead of far over on the left side as melodramatic actors are wont to indicate.

When compared in cross section the shape of the thorax of the human embryo is seen to be decidedly different from that of the adult (Fig. 450). In the embryo the dorso-ventral diameter exceeds that from side to side. In the human adult, on the contrary, where the visceral weight exerts a pull parallel to the backbone instead of at right angles to it, the greater diameter

of the basket is no longer dorso-ventral, but from one side to the other. The general shape of the thorax can be modified by gymnastic and military exercises, by tight lacing, and by pathological conditions such as are induced, for example, by rickets or tuberculosis.

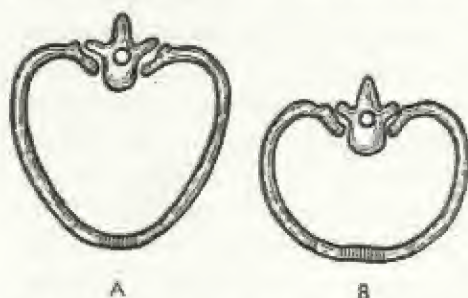


Fig. 450. Cross section through the thorax of a human embryo (A) and a human adult (B). The former resembles that of a quadruped. (After Wiedersheim.)

Quadrupeds in general resemble the human embryo with respect to the relative dimensions of the thoracic basket, which are correlated with the weight of the hanging viscera that exert a mechanical pull downward from the backbone towards the sternum.

Reptiles whose bellies drag upon the ground, as well as such animals as sirenians and cetaceans whose viscera are supported in part by the surrounding medium of water, have a flattened thoracic basket like that of adult bipeds.

2. Ribs

The ribs, which have been of particular human interest ever since the days of the Garden of Eden, are the most conspicuous part of the thoracic basket. They vary in length from mere immovable tips attached to the transverse processes of the vertebrae to hooplike bands of bone entirely encircling the body. Primitively and embryologically there is a pair of ribs for every vertebra from axis to tail. Some fishes have two pairs to a single vertebra. The general tendency, however, both ontogenetically and phylogenetically, is towards a reduction in number at either end of the series.

It is known that the ribs of all vertebrates are not homologous structures, since some of them arise in the sheet of connective tissue that separates the dorsal from the ventral metameric muscles of the body wall, while in other instances they develop between the peritoneal lining and these muscles.

A typical human rib is a somewhat flattened bone so bent and twisted that it cannot be made to lie flat without rocking back and forth when placed on a table (Fig. 451). Its slender and somewhat elastic main body is pieced out at the sternal end in mammals with a flexible cartilage, not shown in the figure. At the dorsal end, which joins the thoracic vertebra in two places, are two prominences known as the *head* and *tubercle* respectively, separated from each other by the *neck* which is slightly narrower than the *body*, or the main part of the rib. Both head and tubercle bear

articular facets by means of which the rib plays upon its vertebral support, maintaining its attachment with a minimum of muscular equipment.

Along the inner margin of each rib, for a part of its length at least, is a shallow groove, the *sulcus*, within the protection of which a vein, or artery, and a nerve lie parallel to each other in harmonious safety.

There are normally twelve pairs of ribs in man (Fig. 452), although much evidence from comparative anatomy, as well as from embryology, supports the conclusion that the ancestors of modern man had more. That reduction in the length of ribs is going on is indicated by their obvious degeneration in the posterior region of the thoracic basket, where at least two pairs fail to reach the sternum.



Fig. 451. The fifth right bony rib of man, as seen from below. (After Cunningham.)

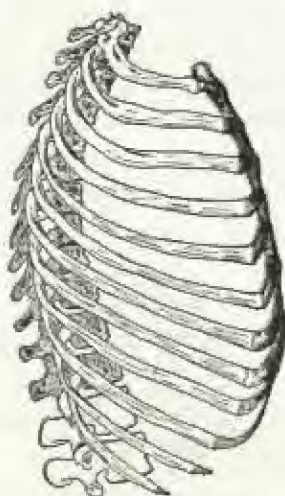


Fig. 452. The thoracic basket. (After Spalteholz.)

To understand the nature of this degeneration it should be stated that all the ribs articulate at one end with thoracic vertebrae, while at the other end only the first seven pairs, or *true ribs*, join the sternum. The remaining five pairs are known as *false ribs*. Of these the eighth, ninth, and tenth secure anchorage to the sternum indirectly by means of the cartilages of the seventh pair of true ribs. Ordinarily the eleventh and twelfth pairs, which are called *floating ribs*, have so far degenerated that they only partially encircle the body, thus failing to make even a vicarious attachment to the sternum.

The ribs of man, therefore, increase in length from the first to the seventh or eighth pairs and then successively decrease to the twelfth pair, which may be reduced to mere stubs hardly more than an inch long.

In medical literature numerous cases are cited of extra human ribs, either at the cervical or at the lumbar ends of the thoracic series, persisting in adult life. Instances are given of a pair of ribs attached to the seventh cervical vertebra, that completely encircled the upper area of the thoracic basket, joining the sternum quite after the manner of true ribs. Persistent cervical ribs, however, are more frequently incomplete, failing of direct sternal attachment (Fig. 453). On the other hand, the first pair of thoracic ribs may sometimes be incomplete (Fig. 454), resulting in a subnormal number. Additional ribs are of more frequent occurrence on the first lumbar vertebra than in the cervical region. Extra lumbar ribs when they appear are called "gorilla ribs" because they represent the normal condition in gorillas and chimpanzees. The closely related gibbons among the apes normally have fourteen pairs, while the orang-utans, like their human kin, have only twelve. The anatomist Rahl in a report upon 640 human bodies examined in the dissecting rooms of the University of Prague says that he found forty of them, or a little more than six per cent, with a gorilla rib on at least one side. Two out of the 640 had only eleven pairs of ribs.



Fig. 453. Cervical ribs (in black) on the seventh cervical vertebra of a human adult individual. (After Lehoucq.)

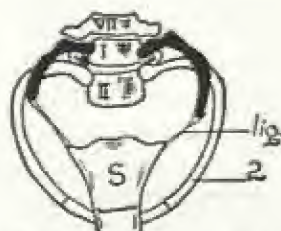


Fig. 454. Reduction of the first pair of ribs (in black) in an adult individual. *lig.*, ligament; *s.*, sternum; *2*, second thoracic rib; *VII*, seventh cervical vertebra; *I*, *II*, first and second thoracic vertebrae. (After Lehoucq.)

Gorilla ribs are about three times more frequent in the human male than in the female, a fact difficult to harmonize with Adam's historic loss. Albertus Magnus (1193-1280), who did not always base his anatomical conclusions upon direct observation, discusses very learnedly the supposed discrepancy in the number of ribs in the two sexes.

With respect to length, the eleventh pair of floating ribs varies from six to eleven inches, while the twelfth pair, ranging from mere stubs less than

an inch long to approximately a foot in length, may nearly encircle the body.

In fetal life ribs are not only present upon the seventh cervical vertebra but also upon all the lumbar vertebrae (Fig. 455). Moreover, rudiments of ribs, which afterwards fuse with the centra to form the lateral masses of the sacrum, are attached to the sacral vertebrae (Fig. 443).

Ribless chordates include amphioxus, the cyclostomes, holocephalans, skates, and such lophobranchs as *Syngnathus* and *Hippocampus* among the teleost fishes. In the ganoid *Polyodon*, the ribs are quite vestigial.

Among other fishes there are two sorts of ribs of diverse origin, namely, *ventral* and *dorsal ribs*, both of which are connected at one end with the vertebral column, although entirely unattached at the other end in the absence of a sternum (Fig. 456).

Ventral ribs simply represent vertebral haemal arches, anterior to the anus, that have spread apart enough to incompletely encircle the body cavity (Fig. 456c). They are therefore sometimes known as *haemal ribs*. They lie entirely inside the muscles of the body wall, next to the peritoneal lining of the body cavity at the points where the myocommata join this layer. The ribs of the dipnoi, as well as of most teleosts and ganoids, are of this character.



Fig. 455. Posterior part of the vertebral column, including three thoracic vertebrae and their ribs. Embryonic lumbar ribs are present on one side, represented in black. (After Wiedersheim.)

Dorsal ribs, on the other hand, grow out from the transverse processes of the vertebrae at the points where the myocommata cross the horizontal septum. They therefore extend between the dorsal and ventral groups of muscles that form the body wall (Fig. 456A). Most elasmobranchs, together with all vertebrates above fishes, have dorsal ribs. In elasmobranchs and modern amphibians these are short and insignificant; but, beginning with reptiles, they become longer, in many instances encircling the body cavity and joining at the ventral ends with the breastbone to form a complete thoracic basket.

There are a few fishes, notably the ganoid *Polypterus*, and certain clupeoid and salmonoid teleosts, which have both dorsal and ventral ribs, one outside the other (Fig. 456B), making two pairs of ribs to each vertebra.

Amphibian ribs like those of all tetrapods are of the dorsal type, although they are never more than mere stubs. In urodeles they are present even on anterior caudal vertebrae which also have haemal arches and therefore are

associated with the homologues of both ventral and dorsal ribs. In no modern amphibian do the ribs encircle the body cavity, but in the fossil stegocephals strong well-developed ribs occurred. The reduced ribs of modern amphibians are therefore to be regarded as vestigial rather than as primitive structures.

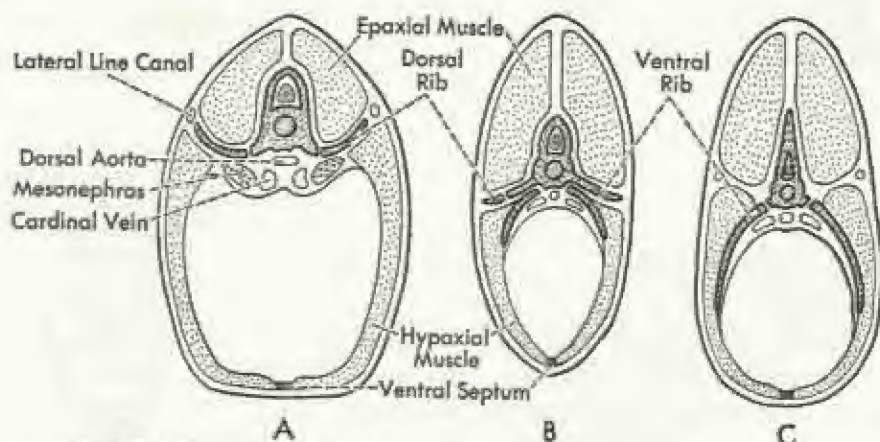


Fig. 456. Diagrams of the three patterns of rib arrangement. A, elasmobranch with dorsal ribs; B, ganoid with both dorsal and ventral (haemal) ribs; C, teleost with haemal ribs only. (After Cöppert.)

The short ribs of urodeles are forked at their proximal ends like a letter Y, thus having two points of attachment to the vertebra (Fig. 457), in that way forming a passage-way between the fork and the vertebra, called the *vertebrarterial canal*. A similar canal persists in mammals and even in man, where one branch of the fork becomes the "head" and the other the "tubercle" of the rib (Figs. 451 and 458), thus preventing the large vertebral artery that lies therein from being disturbed when the neck is stretched or twisted about.

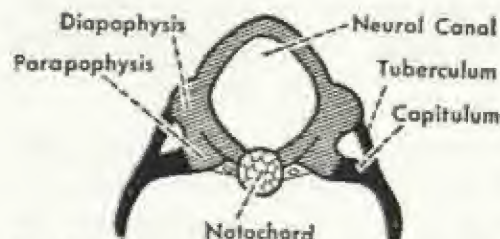


Fig. 457. A vertebra with a pair of ribs (in black) of a young salamander, showing the primitive double articulation of ribs to vertebrae. (After Gegenbaur.)

The ribs of the Anurans are not forked, and become small immovable tips attached to the transverse processes of the vertebrae.

Among reptiles the ribs found in lizards and crocodiles are most typical, becoming differentiated into a dorsal bony *vertebral division*, homologous

to the rib of the urodele and a ventral cartilaginous *sternal division* that attaches to the sternum, which is something entirely new in costal devices. Some lizards and crocodiles even have a third bony segment intercalated between these two parts.

As there is no sternum in snakes all the ribs are "floating," which makes it possible for them to aid materially in locomotion, because the snake grips the ground with its ventral scales and with the ends of its movable floating ribs.

Turtles do not have cartilaginous sternal elements in their ribs. Instead, the bony vertebral parts, which flatten out and join together, are overlaid by dermal costal plates to form part of the dorsal shell, or *carapace* (Fig. 439). In *Sphenodon*, that "living fossil" of New Zealand, there are several unusual ribs in the tail region, which suggests an ancestral prodigality of ribs not characteristic of more modern vertebrates.

As might be expected, birds present extreme modifications in their ribs. Both the sternal and vertebral parts are entirely ossified, making a firm but withal expansible thoracic basket for the attachment of the powerful muscles of flight. This necessary firmness or solidarity is further enhanced by the fact that most of the ribs are "true," that is, connected with the sternum, while in the sacral region the ribs fuse solidly with the vertebrae to form the large strong characteristic "backpiece," or *synsacral complex*, that is so effective in the support of the body weight. The ribs of birds are thin and flat, affording ample surface for muscle attachment, and in addition they are usually provided with light flat supplementary *uncinate processes* (Fig. 459), which serve to splice the ribs of the thoracic basket together into a firm resistant unit for the attachment of flight muscles.

In *Archaeopteryx*, the oldest known fossil bird, the ribs were rounded instead of flat, like those of lizards, and lacked uncinat processes, although *Sphenodon*, crocodiles, and some fossil amphibians, such as *Eryops*, show these supplementary costal inventions.

In mammals the sternal part of the ribs remains cartilaginous in adult life, thus allowing greater freedom in respiratory movements. The total number of ribs in mammals varies from nine pairs in the bottle-nosed whale, *Hyperoödon*, to twenty-four in the primitive two-toed sloth, *Choloepus*, of

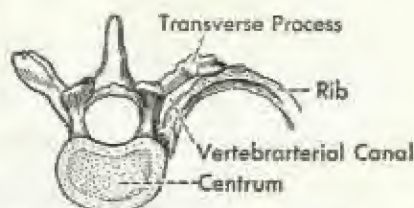


Fig. 459. Diagram to show articulation of rib with both centrum and transverse process of vertebra, thus forming the vertebral canal. (After Weber.)

South America, which finds an elongated thoracic basket useful since it spends most of its time suspended upside down from the limbs of trees.

True ribs, that reach the sternum directly by means of their own cartilage segments, vary from two pairs in the sea-cow *Trichechus*, to ten pairs in the agile spider monkey *Ateles*.

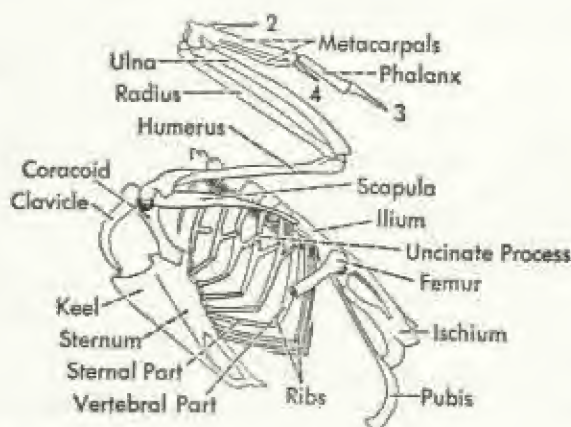


Fig. 459. A part of the skeleton of a goose, showing uncinate processes. (After Kingsley.)

3. The Sternum, or Breastbone

As contrasted with the backbone the frontbone, or *sternum*, is the terrestrial part of the thoracic basket, that is it appears first in the evolutionary history of vertebrates that locomote on land.

The need of such a strengthening structure to knit together the whole thoracic basket into a firm skeletal unit on which the muscles of the anterior legs or arms may find suitable anchorage, is not apparent for the more primitive water-dwellers like fishes that go forward by lateral tail motion rather than by the leverage of bilateral appendages.

Not only fishes are devoid of any kind of sternal apparatus, but also some of the lowest urodeles, for instance, *Proteus* and *Amphiuma*, as well as the footless caecilians, snakes, and turtles.

The sternum develops in the ventral median septum of the anterior trunk or thoracic region of tetrapods. In amniotes it forms the ventral element which, with ribs and vertebrae, completes the thorax. The earliest structure recognized as a sternum is found in urodeles. In *Necturus* (Fig. 460) it is a rather insignificant appearing, irregular mass of cartilage extend-

ing over several segments in the ventral septum and with branches running into adjacent myosepta. Here it seems to arise independent of other parts of the skeleton such as ribs and pectoral girdle. In other urodeles and lower anurans it is a more compact plate of cartilage near the posterior part of the girdle (Fig. 461).

In *Rana* and other higher anurans the sternum consists of several midventral elements unpaired in the adult (Fig. 462). In the mid-line between the two halves of the pectoral girdle is an *epicoracoid cartilage*, ordinarily considered a part of the girdle but also actually in line with the structures usually recognized as belonging to the sternum. At the anterior end of the epicoracoid is an *omosternum* the basal part of which is ossified. A similar cartilaginous and bony *xiphisternum* is connected to the posterior end of the epicoracoid. It is debatable whether or not this posterior part corresponds to the cartilaginous plate of lower Amphibia, although many authors call its bony part the archisternum. These parts all arise as paired structures which subsequently fuse.

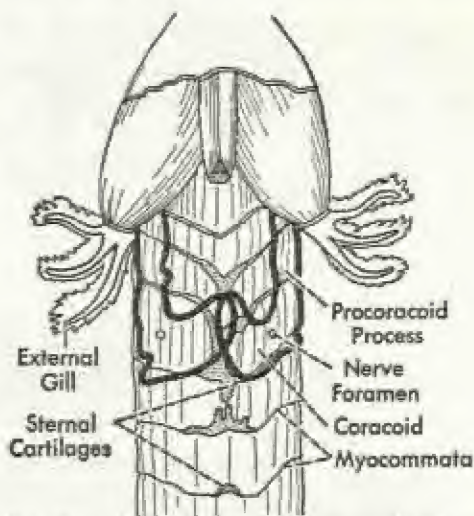


Fig. 460. Ventral view of *Necturus* showing sternal cartilages, extending into myocommata, and pectoral girdle drawn in heavy outline. (After Wiedersheim.)

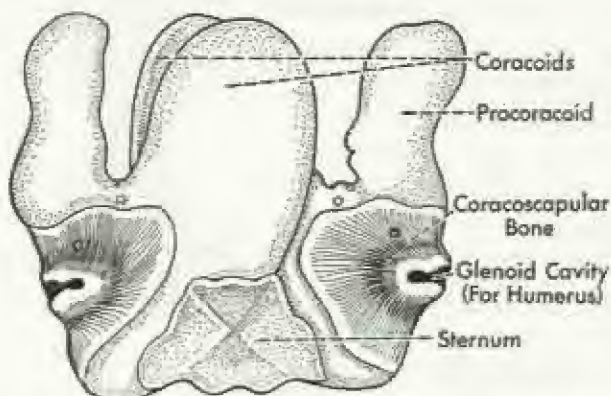


Fig. 461. Pectoral girdle and sternum of *Amblystoma*, ventral view. (After Wiedersheim.)

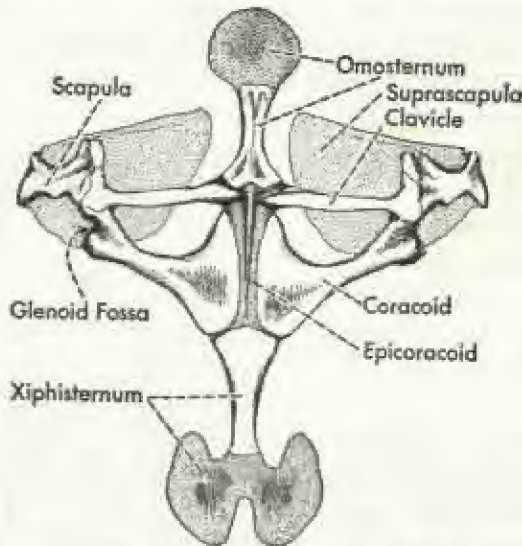


Fig. 462. Sternum and pectoral girdle of a frog, *Rana*, ventral view. Cartilage stippled. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

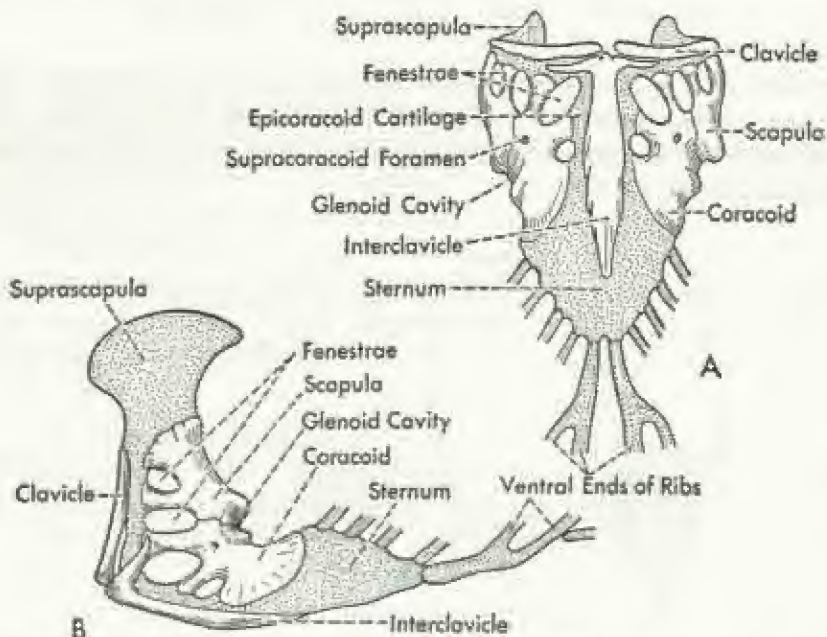


Fig. 463. Sternum and pectoral girdle of *Iguana*. Cartilage dotted. A, ventral view; B, left lateral view. (After Goodrich.)

In Lacertilia (Fig. 463) and Crocodilia (Fig. 464) there is an oblong, cartilaginous plate continuous with which are usually two hornlike, posterior processes. To the anterior end of the sternum the pectoral girdle is attached. Ribs connect with the sides and with the posterior horns. These animals may have been the first to have the ribs attached to the sternum, although some palaeontologists have suggested the possibility that the ribs of *Stegoccephalia* reached such a midventral structure. Snakes and turtles are without sterna.

Birds have a large thin sternum of replacing bone that affords attachment for the pectoral muscles of flight. It is spread out flat in running birds (ratites), but in all flying birds (carinates), a *carina*, or keel, projects at right angles to the breastbone proper, furnishing considerable additional surface for muscle attachment. The pectoral girdle and bony sternal divisions of the ribs attach to the sternum. A comparison of the keels on the breastbones of an albatross, a pigeon, and a hummingbird (drawn to the same scale in Figure 465) shows how large a relative surface for muscle attachment is necessary to enable the tiny hummingbird to maintain its marvelous vibrating wing movements, which are so rapid that the wings themselves, like the spokes of a swiftly rotating wheel, blend out of sight.

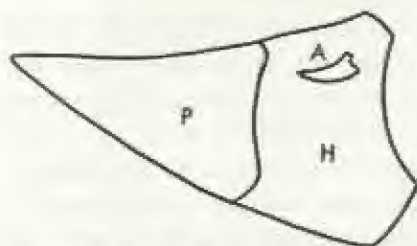


Fig. 465. Comparison of the keel of the albatross, A, pigeon, P, the hummingbird, H, supposing all to have an equal spread of wing. (After Lucas.)

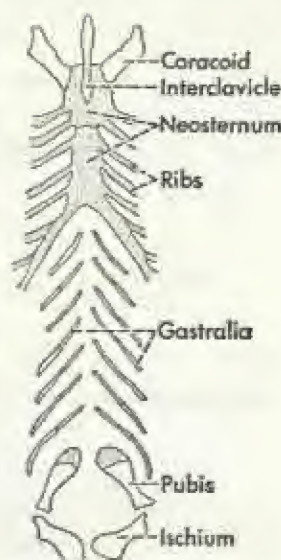


Fig. 464. Sternum, gastralia and parts of the girdles of the alligator. Ventral view. (After Gegenbaur.)

A carina is also a characteristic of extinct flying reptiles (pterosactyls) as well as of flying bats, and in burrowing moles among mammals, although in this latter case it is probably not homologous with the carina of birds.

In mammals the sternum typically consists of a series of six to nine *sternebrae*, composed of replacing bone, followed by a small cartilaginous process (Fig. 466). To the anterior-most of these elements, called the *manubrium*, is attached the first pair of ribs. The other pairs of true ribs attach at the junctions between sternebrae. The posterior part of the sternum is

the *xiphoid cartilage*. In Sirenia and some Cetacea the sternum is a single bony plate.

In the human adult the sternum consists of three parts, namely, the *manubrium*, the *gladiolus* formed by the fusion of four sternebrae, and the *xiphoid*, or *ensiform, cartilage* (Fig. 467). Of these parts the first two are formed of bone, and the last, as its name implies, of cartilage. Its superficial resemblance to a Roman sword explains why the names "*manubrium*," or hand-grip, and "*gladiolus*" and "*ensiform*," both of which signify a sword, were applied to its component parts by the early anatomists. The clavicles and the first seven pairs of ribs are attached to the sternum.

The shortening of the human sternum, which results in the conspicuous notch on the front side of the thoracic basket, follows the fusion of the sternebrae and the consequent disappearance of the intersternal cartilages. It goes further in the female than in the male, thus allowing

a relatively larger unhampered space between the sternum and the pelvis for the accommodation of a possible fetus during pregnancy.

It is now generally agreed that in mammalian embryos the earliest recognizable evidence of the sternum is a pair of ventral, longitudinal precartilaginous bars in front of which lies a single, oval mass of precartilage (Fig. 468). Each bar soon fuses with the oval mass and is in turn joined by the ventral ends of the true ribs of its side of the body. Beginning at their anterior ends the two bars gradually fuse to form a single, median cartilaginous rod. Then centers of ossification appear, usually a single one for the manubrium and a pair for each of the other sternebrae. Perhaps the manubrium is derived from the originally oval, unpaired, anterior element. The mammalian sternum, therefore, arises independent of the ventral ends of the ribs but near these structures. In reptiles and birds the sternum also arises from two longitudinal bars which, even in the earliest observed precartilaginous stage, are continuous with the ribs. The sternal elements of

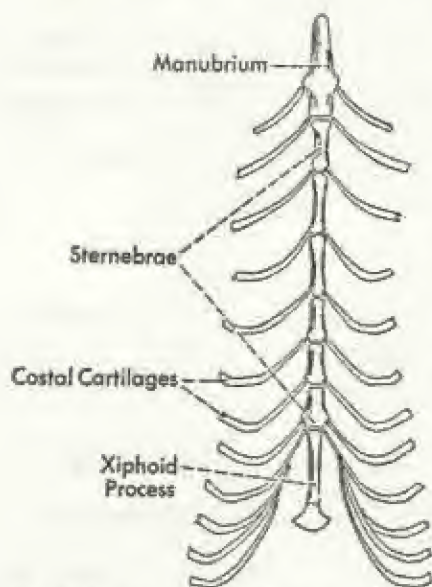


Fig. 466. Sternum and rib cartilages of a cat, showing separate sternebrae. (From Wülder, *History of the Human Body*, copyright 1923, by permission of Henry Holt and Company, publishers.)

modern amphibians are associated with the median part of the pectoral girdle but never with ribs. There has been considerable conjecture as to whether or not the extinct primitive Amphibia (Stegocephalia) had long cartilaginous ventral continuations of their ribs which reached the mid-ventral region to join a cartilaginous sternum. Unfortunately cartilaginous elements do not lend themselves to fossilization.

Three main theories have developed concerning the origin and homologies of the sternum. According to the *Girdle Theory* a mid-ventral part of the pectoral girdle has separated from the rest of that structure, elongated, and become the sternum. Neither embryology nor comparative anatomy can offer much to support this concept. The *Rib Theory* derives the sternum from the ventral ends of the ribs. As noted above, there is some support for this from studies of the development of the amniotes. The fact that the origin of the mammalian sternum can be traced back to pre-cartilaginous structures independent of the ribs casts a shadow of doubt on this theory. Also the situation in the Amphibia offers something of a problem. Some have tried to meet this difficulty by suggesting that primitive amphibians had long ribs which reached the ventral side and gave rise to the sternum, although there is no really good evidence of this from paleontology. Furthermore there can be no doubt that the amphibian sternum arises in ontogeny



Fig. 467. The adult human sternum. (After Spalteholz.)

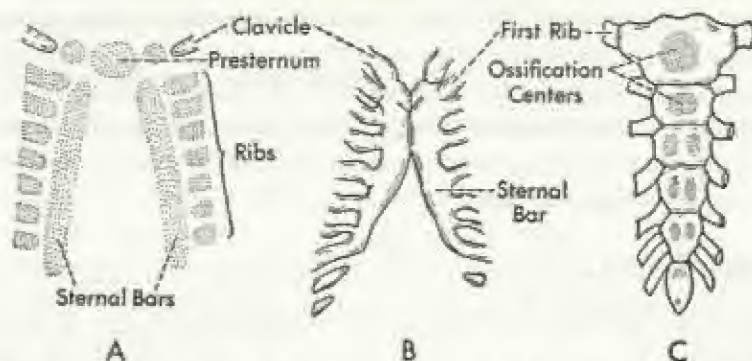


Fig. 468. Development of human sternum. A, early stage; B, cartilaginous stage of a nine-week embryo, halves uniting with one another and with ventral ends of ribs; C, sternum of a child, showing centers of ossification which are at first paired. (A, after Kingsley; B and C, after Arcy.)

completely independent of definitive ribs. Some advocates of this theory apply it only to amniotes and consider the amphibian sternum derived from the girdle region. According to this concept the amniote sternum (*neosternum*) is a new (*neo*, new) structure not homologous with the primitive one (*archisternum*) of amphibians.

The third, and possibly the most plausible theory, assigns an *Independent Origin* to the sternum. With the development of legs and the migration onto land, new stresses develop and the need arises for both additional protection of the ventral body wall and greater surface for the attachment of appendicular muscles. Under these conditions the sternum appears as a modification of the general connective tissue of the mid-ventral region. Both in amphibians and in mammals it has been observed to develop independent of both ribs and girdle. Careful study using new techniques may enable us to recognize sternal elements of reptiles and birds in earlier stages than has been possible to date. All we know now is that the ribs and sternum of these animals are in continuity with one another when first detectable. There is no evidence that either ribs give rise to sternum or sternum to ribs. According to this theory of the independent origin of sternal elements, their connection with the pectoral girdle or ribs or both should be considered as secondary and due to proximity rather than the derivation of one part from the other.

VI. GASTRALIA

In the ventral abdominal region, left unprotected by sternum and ribs, a series of skeletal structures known as *Gastralia* ("Abdominal ribs" or *Parasternum*) is found in *Stegocephalia*, *Sphenodon*, some lizards, *Crocodylia*, and *Archaeopteryx* (Fig. 464). Developing in the ventral parts of the myosepta, they do not meet in the mid-line except in *Sphenodon* and some of the lizards. They may be homologous with the sternal parts of ribs or with the sternum, hence the various synonyms. On the other hand, they may have arisen as the result of local stresses in the abdominal region of some of these heavier, crawling land animals.

VII. THE SKULL

When one takes in his hand a bare human skull (Fig. 469), which during life was never exposed to the light of day, and views it thoughtfully from all angles, as Hamlet viewed poor Yorick's skull, it invites contemplation. Only the uninitiated and thoughtless shudder and turn away. The moralist is reminded of the inevitable end of every human life; the artist sees in it a complex of continuous curving lines that spell grace and beauty;

while the comparative anatomist realizes that he has before him the culmination of countless adaptations, the age-long grist of a tireless evolutionary mill.

The skull of higher vertebrates is a double structure, as shown by its embryology and morphology, as well as by its physiology, and its biological study should be undertaken from these three aspects.

Embryologically it is made up of two sets of bones of diverse origin, an outer and an inner set supplementing each other. In the course of development these two kinds of bony elements join together into a unified whole and are no longer distinguishable as of two kinds.

Morphologically one skull of the double structure, the *neurocranium*, surrounds the brain end of the neural tube, while the other, the *splanchnocranium*, similarly encircles the anterior end of the splanchnic tube, or the digestive tract (Fig. 231).

Physiologically, the two fundamental functions of support and protection are both provided for by the skull, so that it may truly be said to serve at least a double purpose.

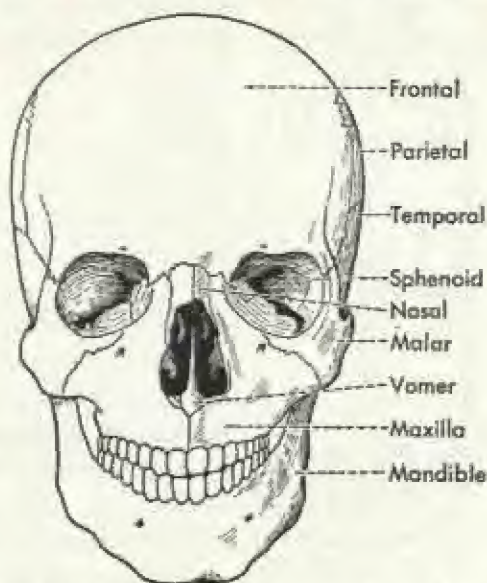


Fig. 469. Face view of human skull. (After Spalteholz.)

1. The Development of the Brain Case

A complete sketch of the rise and union of the two embryonic skulls that become one in adult life may, for clearness of description, be divided into a series of arbitrary stages that pass continuously from one into the other. These stages are: (1) notochordal; (2) underpinning; (3) fusion; (4) upgrowth; (5) roofing-over; (6) shingling; (7) ossification; (8) union; and (9) bone-complex. They are fairly well represented in the adult condition of various vertebrate types, extinct as well as living, and although they have their counterpart in the developmental stages of the human skull, the parallel is by no means exact or complete.

Beginning with the *notochordal stage* (Fig. 470) one observes that just as the brain lags behind the formation of the nerve cord, so the first evidences

of a future skull do not appear until after the notochord is well established. Before any skeletal elements except the notochord are present, the brain is surrounded by a thin, tough, membranous sac which is later replaced by the dura mater and by the skull itself. The anterior tip of the notochord lies just

behind the hypophysis and beneath the midbrain. There are also present three pairs of conspicuous sense organs, arranged along the sides of the brain like devices on the instrument board in an automobile. These sense organs, the olfactory pits, eyes, and ears, are as yet without skeletal support.

At this early stage the anterior enlargement of the nerve tube, that is destined to become the brain, extends horizontally in front of and beyond the end of the notochord without any skeletal platform to support it. This urgent need is soon met, however, in the *underpinning stage* by the appearance of two pairs of independent flat cartilages that form not only a sort of floor upon which the rapidly developing brain may rest, but also furnish something solid to which the important jaw muscles can be attached. One pair of these cartilages, the *parachordalia*, is placed under the posterior part of the brain on either side of the tip end of the notochord, while the position of the other pair, the *prechordalia* or *trabeculae*, is more anterior (Fig. 471). At this time the sense organs also acquire the protection of delicate cartilaginous sensory capsules, the *olfactory*, *optic*, and *otic capsules* associated with the nasal pits, eyes, and internal ears respectively.

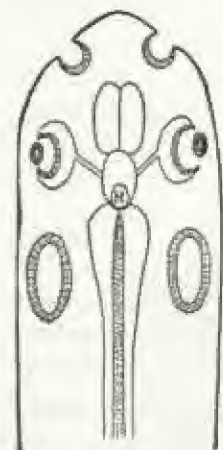


Fig. 470. Diagram of the notochordal stage of skull development, seen from the ventral side. The notochord (dotted) lies along the nerve cord and brain as far forward as *h*, the hypophysis. Three pairs of sense organs, nose, eye, and ear, have appeared, but as yet are without skeletal support. (After Wilder.)

The four primitive cartilaginous floor-boards are at first quite independent, not only of each other, but also of the end of the intruding notochord, and of the six sensory capsules. Marginal growth, however, speedily results in their coming into contact and eventually coalescing as a single continuous plate which encloses at its posterior end the tip of the notochord and joins with four of the six capsules. This constitutes the *fusion stage* (Fig. 472).

The manner of "fusion" with the sense organ capsules is different in the case of each pair, due to the fundamental difference in the kinds of stimuli that the various future sense organs are destined to receive. Thus, the *otic capsules* of the inner ears, which are attuned to respond to vibratory contact with sound waves that can be transmitted easily through an envelop-

ing protective case, are entirely surrounded by and embedded in skeletal cartilage except for the passage-way left for the auditory nerve.

The *eyeball capsules*, on the other hand, which need to be able to rotate freely within their future orbital cavities in order to be directed towards light coming from any direction, do not fuse at all with the rest of the skull but retain their independence in the form of the outer tough *sclerotic coat* of the eyeballs.

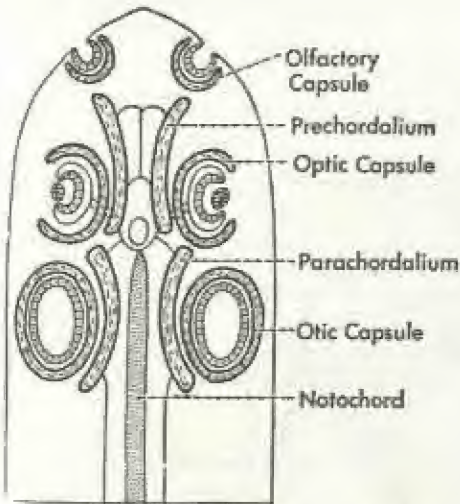


Fig. 471. Diagram of the underpinning stage of skull development seen from the ventral side. The brain now rests upon the prechordalia and parachordalia, while each pair of sense organs is supported by capsules. (After Wilder.)

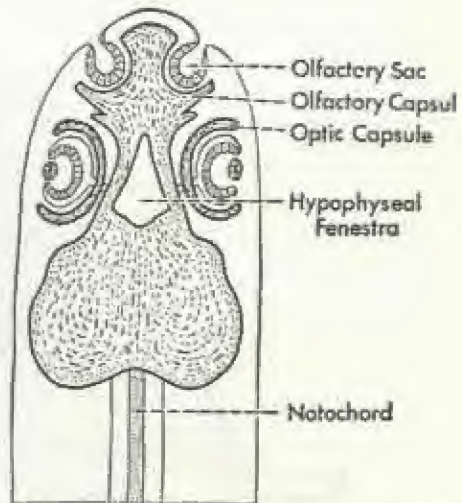


Fig. 472. Diagram of the fusion stage of skull development, seen from the ventral side. The prechordals and parachordals have fused together into a continuous platform involving the cartilaginous supports of the nose and ears and the end of the notochord. The eyeball capsules remain independent as parts of the sclerotic layers of the eyeballs, thus making possible the movements of the eyes within the orbits. (After Wilder.)

Lastly, the *capsules of the olfactory pits* fuse solidly on their posterior and inner surfaces with the skull itself, although perforated by the brushlike olfactory nerves from behind. On their outer surfaces they remain open like cups for the reception of odorous gases, since these chemical stimuli, in order to produce a reaction, must come into direct contact with the nerve endings within the cups.

In the center of the platform there is at first an opening, the *hypophyseal fenestra*, around the developing pituitary body. Later the cartilage grows



Fig. 473. Upgrowth stage of skull development as seen from the left side. (After Roule.)

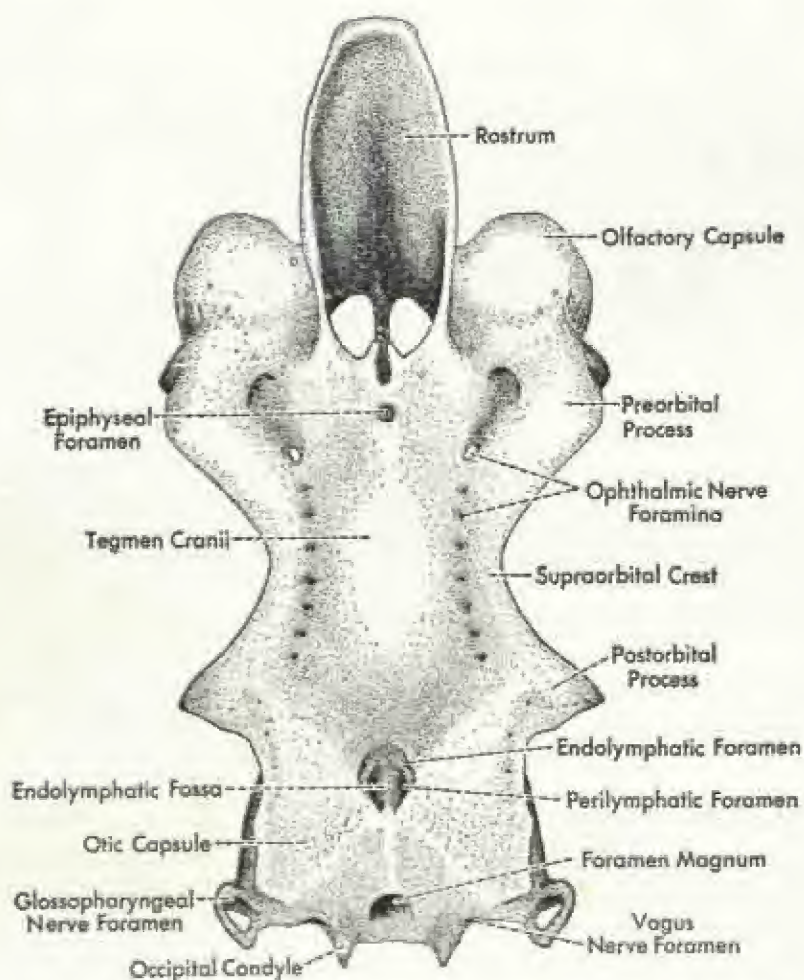


Fig. 474. Dorsal view of the neurocranium of *Squalus acanthias*. (From Sayles, *The Spiny Dogfish, Squalus acanthias*.)

down and around the ventral side of the pituitary to complete the floor of the brain case.

The platform thus assembled by fusion serves not only for support but also as protection for the brain on its under side. The protective function is soon extended to include the sides of the brain by the growth upward of the platform at its edges and in between the sense organ capsules (Fig. 473). This is the *upgrowth stage* in which the roofless skull somewhat resembles a trough or a deep spoon in the bowl of which the brain lies.

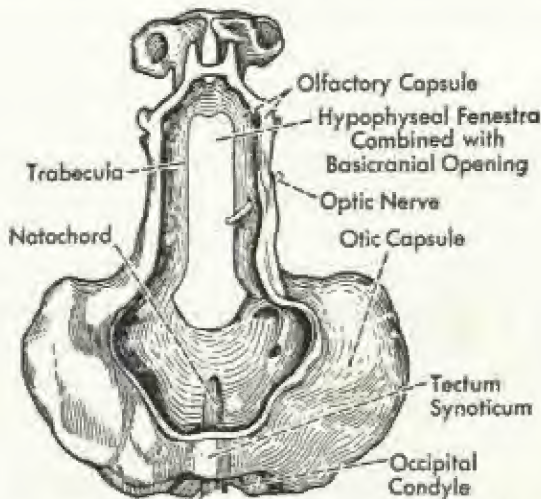


Fig. 475. Neurocranium of a urodele larva, in dorsal view. (After Wiedersheim.)

Growth at the margin of the developing cartilaginous skull case continues until the edges meet above and fuse together in the *roofing-over stage*, thus completing, at least in primitive vertebrates, a protective skeletal envelope around the brain. The skull of the dogfish, for example (Fig. 474), is a continuous cartilaginous casket surrounding the brain, with no sutures to demark its separate components. It is pierced by various small foramina through which the cranial nerves find exit and blood vessels pass in and out, while at its posterior end there is a large conspicuous opening, the *foramen magnum*, through which the nerve cord extends. In bony vertebrates it frequently happens that the cartilaginous roof is limited to a narrow band extending over the extreme posterior part of the brain to form a ring around the foramen magnum (Fig. 475). As a result a different sort of roof is developed for most of the skull.

Thus far only the formation of the *inner skull* has been touched upon.

The stages that follow concern the origin of the *outer investing skull*, and the final modification and union of the two skulls into one.

After the formation of the inner cartilaginous envelope just described, or even before that process is complete, the inner skull becomes partially overlaid by certain definite bony elements which are not previously marked out in cartilage but instead are formed directly as bone out of dermal membrane. This may be called the *shingling stage*. Ordinarily the bony "shingles"

do not fuse together so completely as to lose their identity, but rather join, each one to its neighbors, by means of clearly defined immovable joints, or sutures. Together these bones constitute the outer skull.

In the ostracoderms, now regarded as close to the ancestral stock of the vertebrates, the head was quite completely covered by numerous scale-like bones which were not particularly different, except in their enlarged size, from other scales that were found in the trunk and tail regions. The outer skull, therefore, makes its initial appearance as an exoskeletal armor of separate scaly plates, loosely shingled over the inner cartilaginous brainbox. The fully formed skulls of *Acipenser* (Fig. 476) and other cartilaginous ganoids (*Chondrostei*) are in the shingling stage.

Centers of ossification, forming the *ossification stage*, soon appear in the inner cartilaginous skull, particularly around the foramina for the exit of the delicate nerves where protection is especially needed. What was at first a continuous cartilaginous encasement for the brain thus becomes gradually replaced

by definite separate bones, which increase rapidly at their margins, thus allowing the entire structure to accommodate itself to the enlarging brain within. Finally, the new replacing bones of the inner skull, like the scaly investing bones of the outer skull, join together in sutures and fusions. Skulls in this stage of development occur principally among the bony ganoids of which there were abundant species in Devonian times. The bowfin, or *Amia* (Fig. 477), is a modern representative. The process of ossification of the inner skull, initiated in the ganoids, is more completely carried out in amphibians and reptiles. Fossil skulls of lower vertebrates leave much to be desired by way of supplementing our embryological knowledge of the course of events for the reason that usually the important cartilaginous parts have not been preserved.

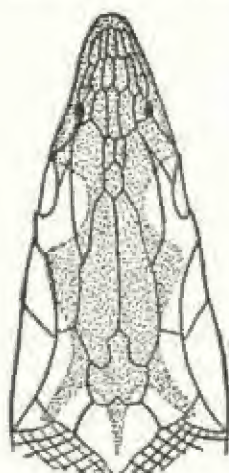


Fig. 476. The skull of a sturgeon, *Acipenser*, showing the inner cartilaginous skull (dotted) and the outer skull of bony scales. (After Gegenbaur.)

Following the ossification of the cartilaginous inner skull, the outer dermal skull bones sink deeper in from their former external scalelike position, and, becoming overlaid with skin, are grafted inseparably to the bones of the inner skull. This is the *union stage*. A single skull is now all that is visible, for there is no way, except by tracing the mode of embryonic origin, to distinguish the *investing bones* of the outer skull from the *replacing bones* of the inner skull, since both present the same appearance as to texture. These embryonic stages of the union of two skulls in vertebrates are paralleled by the adult skulls of various amphibians and reptiles. The two skulls of the union stage are not brought in all cases into such close contact with each other that their dual character is obliterated. In the turtle (Fig. 481) for example, the doubleness of the skull is evident, although the inner part immediately around the brain and the vaulted roof above it do not strictly correspond to the inner and outer skulls described by the embryologist. The large outer roof of the turtle's skull provides adequate surface for the attachment of the head muscles, particularly those of mastication, rather than space to accommodate the brain, which is disappointingly small.

The final phase in the embryonic development of the cranium is the *bone-complex stage*. It results from the fusion of neighboring bones into complexes that thereafter pass for single bones. Thus, the sphenoid bone in the adult human skull is a combination of at least ten different embryonic bones, namely, the *basi-* and *presphenoids*, which are represented throughout life in most vertebrates as single bones although arising respectively from two centers of ossification; and the paired *orbitosphenoids*, *alisphenoids*, *pterygoids*, and the *median lamellae*.

Since a light, strong brain case is desirable for purposes of flight, the process of bone-complex formation in the avian skull has gone to so great an

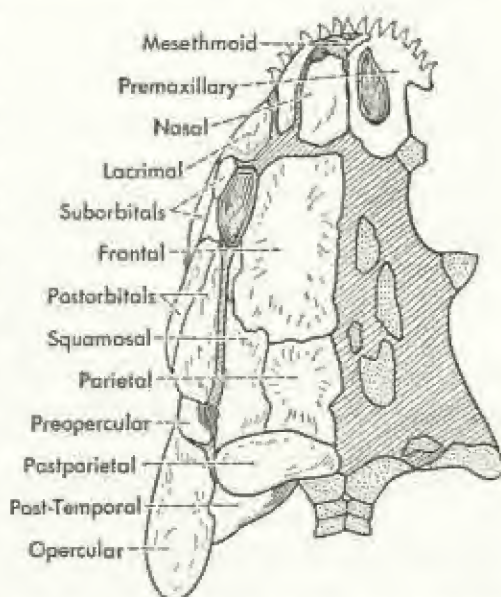


Fig. 477. Skull of the holostean, *Amia*, as seen from the dorsal side, with the investing bones removed from the right half. (Investing bones in white; cartilage in parallel lines; replacing bones, dotted.) [After Bütschli.]

extreme that most of the sutures become obliterated in the adult bird, giving the cranium the appearance of an almost continuous bone.

In the mammalian skull, as previously intimated, all of the stages described in the preceding paragraphs are not repeated. For instance, the outer, or investing, skull begins its rapid development before the inner cartilaginous skull has been completed, in consequence of which the up-growth and roofing-over stages are largely omitted, being rendered unnecessary since the investing bones prove adequate in forming a roof over the brain. There remain, nevertheless, unmistakable evidences of the dual origin of the vertebrate cranium even in man.

2. The Splanchnocranium

The description of the skull so far given applies solely to the *neurocranium*, which invests the end of the neural tube, that is, the brain. The other morphological half of the skull, namely, the *splanchnocranium*, surrounds the anterior end of the digestive tube in the form of a series of cartilaginous or bony arches which strengthen the walls of the anterior portion of the tube that have been weakened by the respiratory gill slits.

Among the lower water-dwelling vertebrates the splanchnocranium is relatively large and may extend posteriorly farther than the neurocranium, since it furnishes support for the respiratory muscles of the gills. Higher up in the evolutionary scale it becomes more and more reduced. The converse is true of the neurocranium which increases in relative importance with the increasing size of the brain.

The primitive arrangement of the splanchnocranium may best be understood by reference to the skull of *Squalus* (Fig. 231), in which the distinction between the neurocranium and the splanchnocranium is still clearly defined. As will be seen there are present seven cartilaginous arches encircling the anterior part of the alimentary canal, one behind the other, like horseshoes with the open ends up. Each arch is composed of a number of separate elements that articulate with one another with the result that to some extent the arch as a whole may be extended or contracted accordion-fashion, as occasion demands.

The first or *mandibular arch*, which is the most anterior one, is made up of two pairs of separate elements that delimit the mouth. The original horseshoe arch bends back and breaks on either side to form the articular joints of the jaws, as shown diagrammatically in Figure 478. The dorsal elements, or *pterygoquadrate cartilages* (sometimes called the *palatoquadrates*), become the upper jaw while the ventral pair, or *Meckel's cartilages*, form the lower jaw.

In the spiny dogfish (Fig. 231) as well as most other elasmobranch fishes, the second or *hyoid arch*, emancipated like the mandibular arch from bearing gills, serves as a support for the primary tongue and also as a suspensory apparatus, furnishing the only points of articulation between the neurocranium and the splanchnocranium. The tongue support includes a median *basihyal* which runs across the anterior part of the tongue and to each end of which is attached a *ceratohyal*. From the posterior, or embryonic dorsal, end of each ceratohyal, a *hyomandibular* runs medially to attach to the side of the otic region of the neurocranium. The posterior end of the upper jaw is attached at the junction of hyomandibular and ceratohyal.

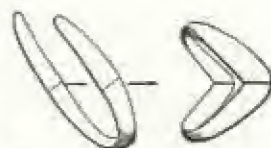


Fig. 478. Diagram to show how the primitive upper and lower jaws form from a horseshoe-shaped cartilaginous arch.

The five posterior arches are *gill arches* that, somewhat in the manner of ribs, extend protectively around the anterior end of the digestive tube (Fig. 479). Between these pairs of arches are gill slits, which allow water

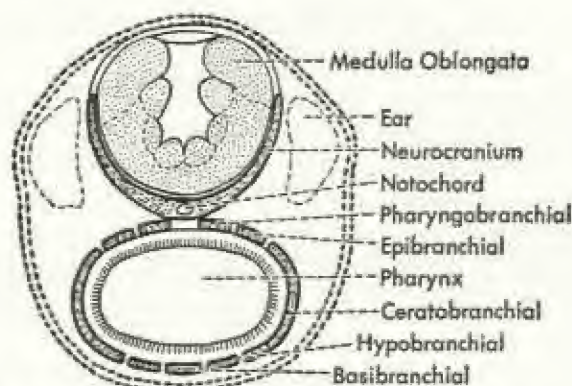


Fig. 479. Cross section diagram of primordial neurocranium and splanchnocranium.

entering the mouth to pass out on either side after bathing the vascular gills that hang suspended from the arches. The gill arches diminish in size posteriorly and in numbers in bony fishes, the loss always coming at the posterior end of the series. In a few of the more primitive elasmobranchs there are present six and even seven pairs of gill arches, but the usual number is five.

In higher vertebrates only the mandibular arch becomes overlaid by investing bony elements which are therefore limited to the upper and lower

jaw regions of the splanchnocranium. In the bony fishes the gill cover, or operculum, of each side of the body consists of four thin flat bones, the *opercular*, *preopercular*, *subopercular*, and *interopercular*.

In the evolution of the higher vertebrates the need for respiratory gills gives way with the rise of the lungs, and gill arches become relegated to what may be called the anatomical scrap-heap. They are not entirely lost, however, even in man, for certain parts of the mature skeleton are directly derived from the primitive splanchnocranium, inherited from ancestral water-dwellers. Thus the legendary history of remote ancestors is retold in the human embryo. Nowhere is the thrift and resourcefulness of Mother Nature better exemplified than in the disposal of those parts of the splanchnocranium that have outlived their original usefulness, owing to the emergence of vertebrates from life in water to land.

3. Types of Jaw Suspension

There are four principal types of attachment of the splanchnocranium to the neurocranium, namely: amphistylic, hyostylic, autostylic, and cranio-stylic (Fig. 480). The first three of these involve the pterygoquadrate, the hyomandibular, or both, while the last-named is associated with investing bones.

Amphistylic suspension occurs when both the pterygoquadrate and hyomandibular make direct articulation with the neurocranium. The pterygoquadrate usually articulates at two points: (1) a *basal process* meeting the ventral side of the neurocranium at the level of the posterior end of the embryonic trabecula, and (2) an *otic process*, at the posterior end of the upper jaw, articulating with the side of the otic capsule. The hyomandibular also articulates with the otic capsule. This type of skull is found in primitive cartilaginous fishes including a few living selachians.

The *hyostylic* method of suspension, as found in most elasmobranchs and all bony fishes, was described above for *Squalus* in which the hyomandibular alone acts as the suspensorium of the splanchnocranium. In the bony fishes a *quadrate* bone develops in the posterior part of the pterygoquadrate while an *articular* bone forms in the portion of Meckel's cartilage which articulates with the quadrate. This hyostylic suspension permits protrusion of the jaws in the prehension of food (Fig. 221).

In *autostylic* skulls, which are found in dipnoans, amphibians, reptiles, and birds, the upper jaw articulates with the neurocranium through two or more pairs of processes without intervention of the hyomandibular. These articulations are usually of the immovable type (*synarthroses*). The hinge-type articulation between the jaws is between the articular of the lower jaw

and the quadrate of the upper jaw, as in the bony fishes. Possibly Holocephali also belong in this category but their entire upper jaw is almost indistinguishably fused with the neurocranium.

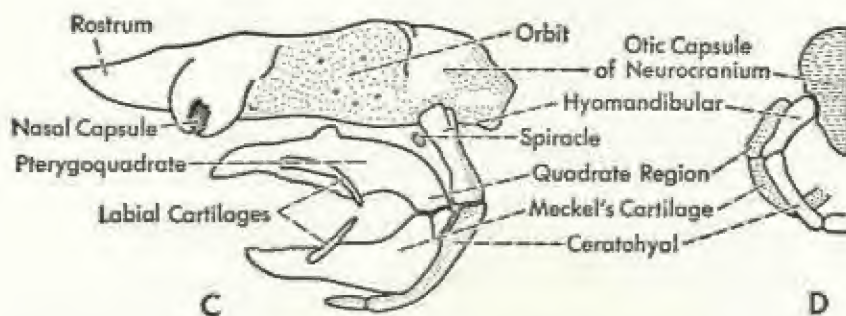
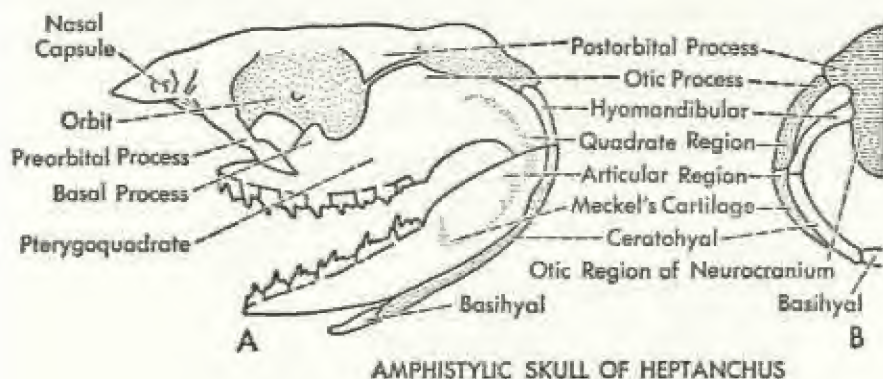


Fig. 480. Diagrams of an amphistylic skull (A and B) and hyostylic skull (C and D). A and C are left-side views; B and D, posterior views of left half. (After Goodrich.)

The *craniostylic* type of skull, found only in the mammals, is a modification of the autostylic type in that the upper jaw articulates directly with other skull elements without any hyomandibular participation. But in the mammals the articular and quadrate bones become transformed into middle ear ossicles (malleus and incus, respectively), while the jaw articulation is taken over for the first time by two pairs of investing bones, the dentaries of the lower jaw and the squamosals of the upper jaw.

4. Comparative Anatomy of the Skull Bones

According to Gregory there may be as many as 180 bones in the skulls of some of the primitive fishes. In amphibia and reptiles the number ranges

from 95 down to 50, with the smaller number in the more recent species. Mammals usually have about 35 skull bones but man has 28 or less, including the middle ear ossicles.

Even though we were to limit ourselves to a consideration of the most important elements of the skull, it would be difficult to follow the evolutionary changes of so many parts at one time. It is preferable, therefore, to give our attention to this complex structure region by region, considering the various parts in the following order:

I. Cartilages or replacing bones of

1. Occipital ring
2. Ventral trough
3. Otic capsule
4. Optic capsule
5. Olfactory capsule
6. Pterygoquadrate
7. Meckel's cartilage
8. Hyomandibular
9. Hyobranchial apparatus

II. Investing bones of

1. Roof of skull
2. Pterygoquadrate covering
3. Ventral surface of skull
4. Meckel's cartilage covering

Throughout the following discussion it should be kept in mind that frequently the homologies of parts are far from certain. Two bones may even bear the same name in different species and yet not be homologous. Because a bone occupies much the same region in a lower vertebrate as another does in a mammal, the former may have been named after the latter. Yet careful studies of the embryonic developments of these parts may show clearly that they have distinctly different origins and consequently are not homologous. Because most of the parts of the cyclostome skull are of doubtful homology, they will not be included in the present discussion.

At the posterior end of the skull an *occipital ring* of cartilage is laid down around the *foramen magnum*, through which the nerve cord is continuous with the brain. In this ring four bones usually develop: a dorsal *supraoccipital*, two lateral *exoccipitals*, and a ventral *basioccipital* (Fig. 481). Modern amphibians, however, have only the *exoccipitals*. In this region there is usually at least one raised surface for articulation with the first vertebra. Such a surface is called an *occipital condyle*. In cartilaginous

fishes there are two of these condyles, one on either side of the point where the notochord enters the skull, while in bony fishes the entire basioccipital region, concave on its posterior end, projects posteriorly to articulate with the centrum of the first vertebra in a joint similar to that between any two amphicoelous vertebrae. Present in all tetrapods, these condyles may occur on the basioccipital, on the two exoccipitals, or on all three of these bones,

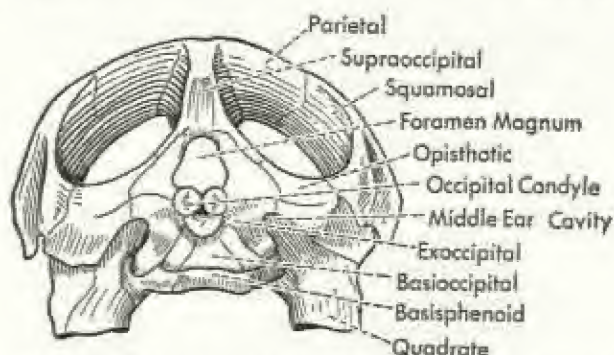


Fig. 481. Posterior view of a turtle's skull. (After Reynolds.)

but not on the supraoccipital. A tripartite condyle, formed by contributions from the basioccipital and exoccipitals, is found in some stegocephalians, the cotylosaurs, and most therapsids, as well as the turtles (Fig. 481), lizards, and snakes among modern reptiles. From this primitive condition there seem to have been three lines of evolution. The modern amphibians, having lost the basioccipitals, have two separate condyles, on the exoccipital bones. Some extinct reptilian groups, as well as the present-day crocodiles and also the birds, have a single occipital condyle on the basioccipital only, the exoc-

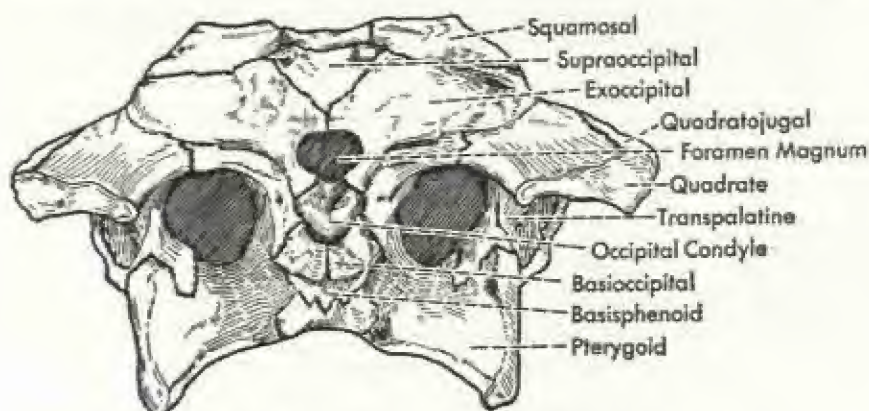


Fig. 482. Posterior view of an alligator's skull.

cipital parts becoming reduced until they do not participate in the condylar surface (Fig. 482). Mammals and the higher therapsids have two condyles, on the exoccipitals only, the condylar region of the basioccipital disappearing although the bone itself is not lost as in amphibians (Fig. 509).

In the *ventral trough* anterior to the basioccipital most mammals develop a row of three unpaired, median bones: *basisphenoid*, *presphenoid*, and *mesethmoid*, with the last-named forming the dorsal part of the nasal septum (Figs. 483 and 500). Extending dorsally into each orbit from the side of the presphenoid is an *orbitosphenoid*. In tetrapods other than mammals the anterior part of the trough usually remains cartilaginous as *presphenoid* and *mesethmoid* bones do not develop.

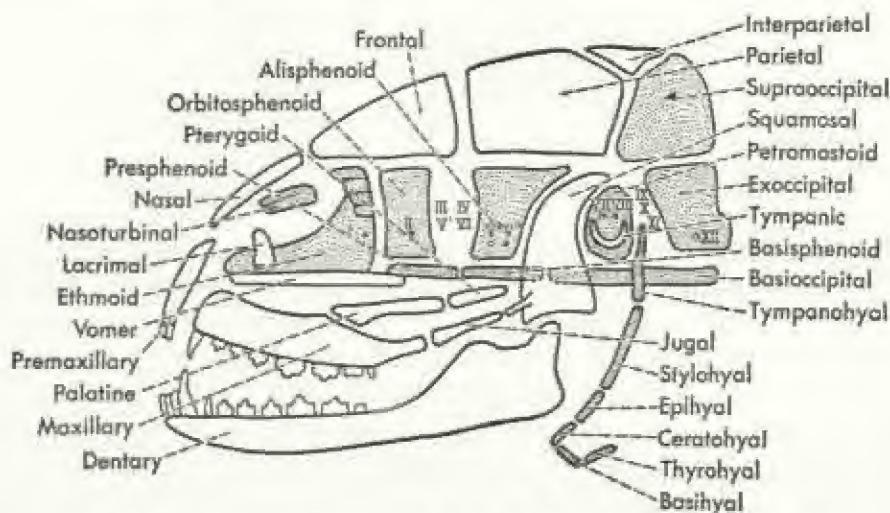


Fig. 483. Composite mammalian skull. Investing bones in outline; replacing bones, dotted. I-XII, locations of the exits of the cranial nerves. (After Weber.)

In the *otic capsule* three bones are commonly laid down: a dorsal *epiotic*; a ventral, anterior *prootic*; and a ventral, posterior *opisthotic*. In mammals these three usually fuse to form the *petromastoid*. In birds the prootic forms most of the ear capsule, while the small opisthotic fuses with the exoccipital, and the small epiotic with the supraoccipital. Among reptiles the prootics are usually separate bones while the opisthotics fuse with the exoccipitals except in turtles (Fig. 481). In Amphibia the prootic and sometimes the opisthotic appear as separate bones (Fig. 484).

As mentioned previously the *optic capsule* does not fuse with the other parts of the chondrocranium. Instead it becomes the *sclerotic cartilage*, pres-

ent in the eyeball of most vertebrates except marsupials and placental mammals. In some reptiles and birds a ring of *sclerotic bones* ossifies out around the cornea (Fig. 485).

In reptiles, birds, and mammals the lateral wall of each *olfactory capsule* usually gives rise to an *ectethmoid* bone from which *turbinal plates* (conchae) extend into the corresponding nasal cavity. In reptiles and birds, in which the olfactory sense is not well developed, these bones are small. In mammals they are much larger, the conchae becoming extensively coiled to fill practically the entire nasal cavity of those species which have a very keen sense of smell (Fig. 681). In man three turbinal plates hang down into each nasal cavity from the lateral wall (Figs. 486 and 677). In most mammals the two ectethmoids fuse dorsally with the median mesethmoid, previously mentioned, to form a single ethmoid bone. At the point of junction of the three parts, the ethmoid bone is flattened out into a *cribriform plate* which forms part of the partition between the cranial cavity above and the nasal cavities below and in front (Fig. 487). This plate is perforated by numerous holes through which the minute branches of the olfactory nerve run from the organ of smell to the olfactory lobes of the brain. Ethmoid is from the Greek and cribriform from the Latin; both mean "sieve-like."

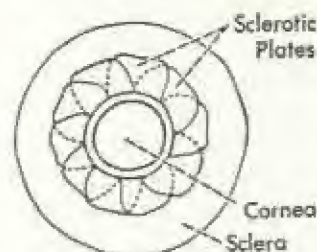


Fig. 485. External view of eyeball of a pigeon, *Columba*, showing sclerotic plates. (After Vogt and Yung.)

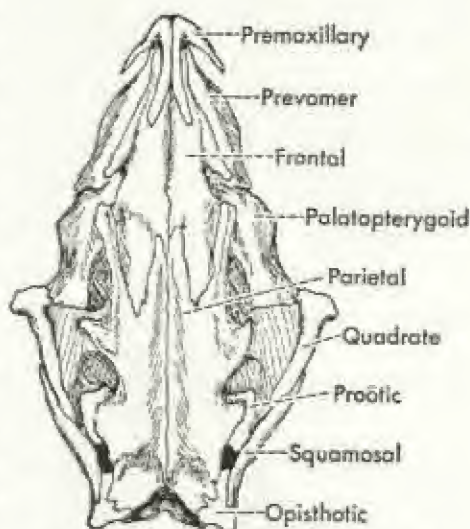


Fig. 484. Dorsal view of the skull of *Neotoma*. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

The *pterygoquadrate* cartilages, which serve as the upper jaw of cartilaginous fishes, give rise to one or two pairs of bones in most vertebrates.

In the quadrate region of all groups below the mammals there is a *quadrate* bone, with which the lower jaw articulates, while in mammals this region gives rise to the *incus*, the second in the chain of three small middle

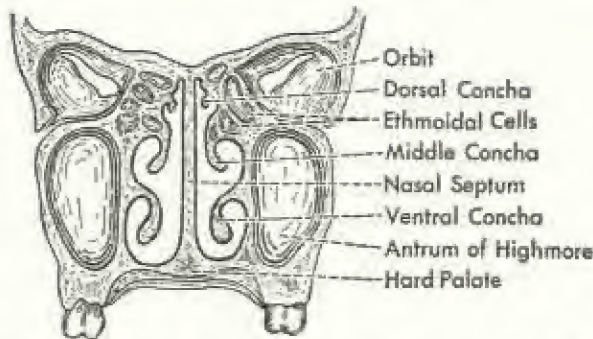


Fig. 486. A vertical cut through the nasal region, showing the ethmoid and turbinal bones heavily outlined in black. (After Tillaux.)

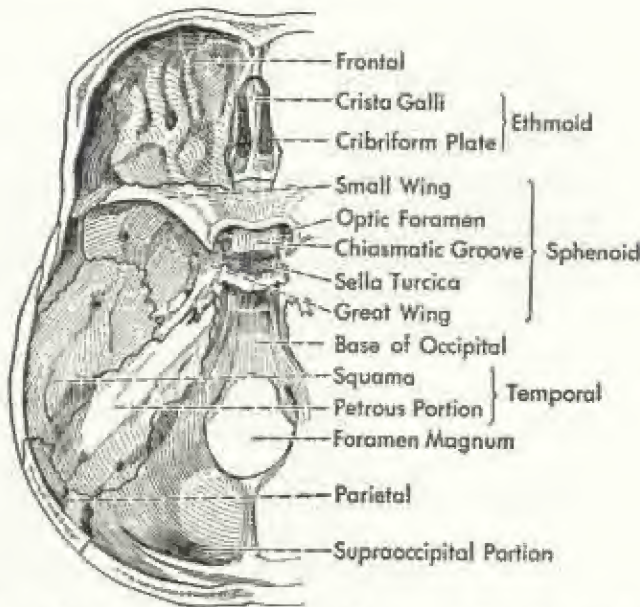


Fig. 487. Internal view of base of human skull. (After Toldt.)

ear bones (Fig. 488). A second pair of bones, appearing in some reptiles and in mammals, is laid down in the *ascending process* of the pterygoquadrate which extends dorsally into the region just in front of the otic capsule (Fig. 489). In reptiles this bone is called the *epipterygoid* (Fig. 490) while in mammals it is the *alisphenoid*.

Meckel's cartilage, the embryonic lower jaw, usually gives rise to an *articular* bone near the angle of the jaws which, as its name implies, articulates with the quadrate of the upper jaw (Figs. 491 and 492). In mammals the articular becomes the *malleus*, the outermost of the three middle ear

bones (Fig. 488). The remainder of this cartilage usually degenerates, its place being taken by investing bones. In some fishes and amphibians, however, one or more additional pairs of bones may develop in the cartilage.

The *hyomandibular* becomes ossified as a bone of that name in the *hyostylic Osteichthyes* (Fig. 491). In the *autostylic tetrapods* it gives rise to the *columella* or *stapes* of the middle ear, transmitting vibrations from the external tympanic membrane to the internal ear in all except mammals. In the latter Class it is the innermost of the chain of three middle ear bones which includes malleus, incus, and stapes (Fig. 488).

The *hyobranchial apparatus*, which includes the five branchial arches and the hyoid arch except the hyomandibular, gives rise in tetrapods to laryngeal cartilages and the hyoid apparatus. In larval amphibians and adult *perennibranchs* these structures, in somewhat modified form, are still associated with gills (Fig. 493A). In the adults of strictly land amphibians the apparatus is reduced to a plate of cartilage from which there extend out several pairs of *horns* (Fig. 493B). Parts of the latter are bony. In lizards (Fig. 493C) and birds (Fig. 235) an *entoglossal process*, part of the basihyal, extends into the tongue. In birds only one pair of horns is well developed. In the amphibians, reptiles and birds small laryngeal cartilages of doubtful homologies occur (Figs. 352 and 353).

In mammals (Fig. 494) the median part of the apparatus is limited to a transverse bar, the *body*, in the base of the tongue. A pair of long *anterior horns*, from the hyoid arch, extends up to the ear regions into which the hyomandibulars have migrated as the stapes, as noted above. A pair of short *posterior horns*, from the first branchial arch, rests against the larynx. The thyroid cartilage of the larynx arises from the second and third branchial arches. Some uncertainty exists about the fate of the fourth and fifth branchial arches although there is evidence that the fourth may give rise to the cartilage of the epiglottis and the fifth to parts of the larynx and anterior tracheal rings.

What becomes of the different elements that make up the splanchnic part of the primitive skull is presented graphically in Figure 495, where the theoretical extent and position of the original arches are drawn as a background for the relics that persist. The same thing is also indicated in Figure 496 and Table VII.

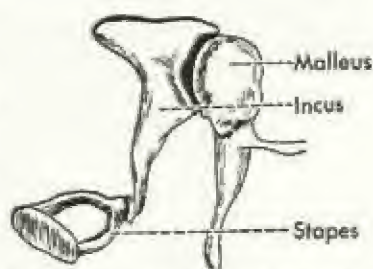


Fig. 488. The bones of the middle ear. (After Henle.)

TABLE VII. Fate of the Visceral Arches (Splanchnocranium)

NUMBER OF VISCERAL ARCH	ELASMO- BRANCHIS	OTHER FISHES	AMPHIB- IANS	REPTILES AND BIRDS	MAMMALS
1	Pterygo- quadrate	Quadrate			Incus
		Unossified portion (covered by investing bones)			Alisphenoid
	Meckel's cartil- age	Articular			Malleus
		Unossified portion (covered by investing bones)			Meckel's cartilage
2	Hyoid arch	Hyo- mandib- ular	Columella, Stapes		Stapes
		Hyoid	Hyobranchial apparatus (in part)		Styloid process External ear cartilages Anterior horn of hyoid
3	First branchial (gill) arch		Part of hyoid apparatus		Posterior horn of hyoid
4	Second branchial (gill) arch		Part of hyoid apparatus		Thyroid cartilage
5	Third branchial (gill) arch		Part of hyoid apparatus		
6	Fourth branchial (gill) arch		Part of hyoid apparatus (?)		Epiglottis (?)
7	Fifth branchial (gill) arch		Laryngeal and tra- cheal cartilages (?)		Arytenoid and cricoid cartilages (?) Anterior tracheal cartilages (?)

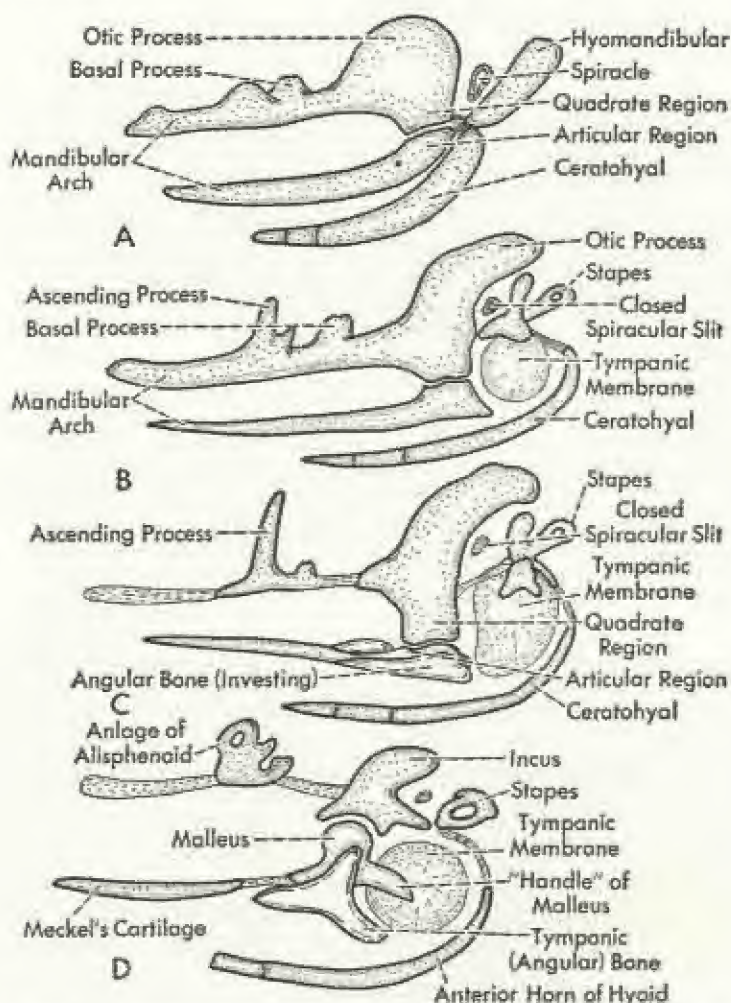


Fig. 489. Diagrams showing the evolution of the mandibular and hyoid arches. A, primitive autostylic fish; B, primitive tetrapod; C, primitive lizard; D, primitive placental mammal. All are left-lateral views. (After Goodrich.)

It will be seen that the embryonic skeletal material, which originally had to do with respiration and the support and protection of the anterior end of the digestive tube, has assumed by a complicated series of makeshifts very diverse functions, such as the support of the vocal apparatus and the muscular tongue, and the transmission of sound waves to the internal ear.

Investing bones make up the *roof of the skull*, a region in which scarcely any cartilage develops in bony fishes and tetrapods. Along the mid-dorsal region, extending from the supraoccipital to the external nares, there is a

double row of bones composed of four pairs, namely: *interparietals*, *parietals*, *frontals*, and *nasals* (Fig. 497). The orbits are usually lateral to the frontals. In front of each orbit may be a more medial *prefrontal* and a more lateral *lacrimal*, behind it a more medial *postfrontal* and a more lateral *postorbital*.

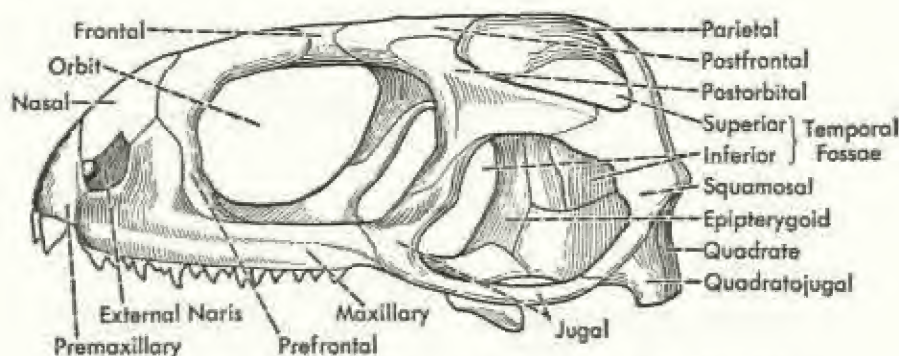


Fig. 490. Skull of *Sphenodon*, left-lateral view. (After Reynolds.)

The interparietals, occurring in many extinct groups, are limited to one present-day Class, the mammals, in which they unite into a single somewhat triangular bone which lies between the supraoccipital and the parietals. Parietals, frontals, and nasals occur in nearly all bony vertebrates, but occasionally at least one pair becomes reduced, by fusion, to a single median bone (Figs. 469 and 498). Lacrimals, prefrontals, and postorbitals are found in lower Osteichthyes, Stegocephalia, cotylosaurs, and therapsids. In addition prefrontals and postorbitals are common among modern reptiles, while lacrimals occur chiefly in crocodiles, birds, and mammals. Postfrontals exist as separate bones only in *Sphenodon* among living tetrapods (Fig. 490).

Although originally bones of the dorsal surface, the *septomaxillaries* (Fig. 498) usually migrate into the nasal cavity to roof over the organ of Jacobson, an accessory olfactory organ in the ventral part of this cavity. These bones are found in nearly all tetrapods except turtles, crocodiles, birds, and most higher mammals, groups in which Jacobson's organ is either poorly developed or absent. In snakes and lizards (Fig. 680) these parts are of considerable size.

The *investing bones covering over the pterygoquadrate* form the ventro-lateral part of the tetrapod skull and articulate dorsally with the lateral elements of the cranial roof. Beginning in the mid-line at the front of the skull they are: *premaxillaries*, *maxillaries*, *jugals*, *quadratojugals*, and *squamosals*. In higher groups these parts are frequently arranged in a single row

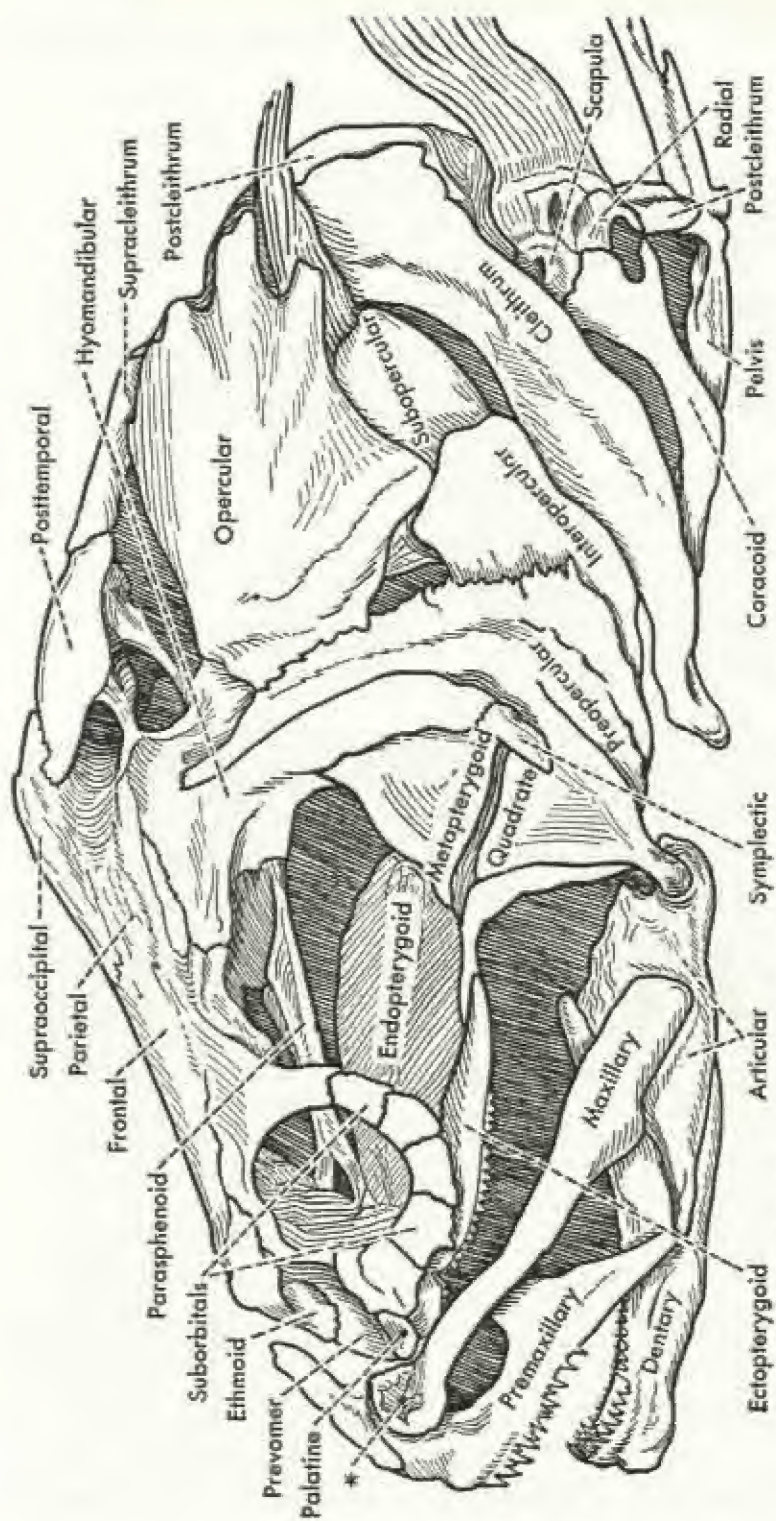


Fig. 491. Skull, girdles, and appendages of a teleost. Premaxillary and maxillary bones have been displaced anteriorly; point marked with (*) would, in life, lie directly medial to point at end of guide line of palatine, branchiostegal rays and some related parts are omitted. (After Sayles.)

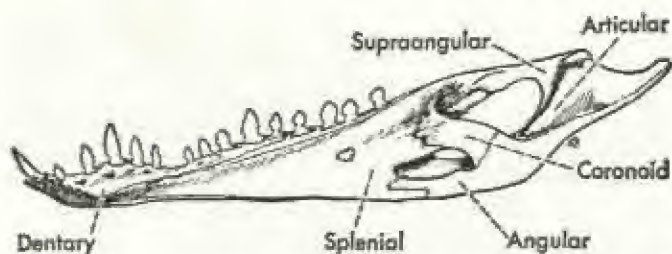


Fig. 492. The lower jaw of an alligator, showing its component bones. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

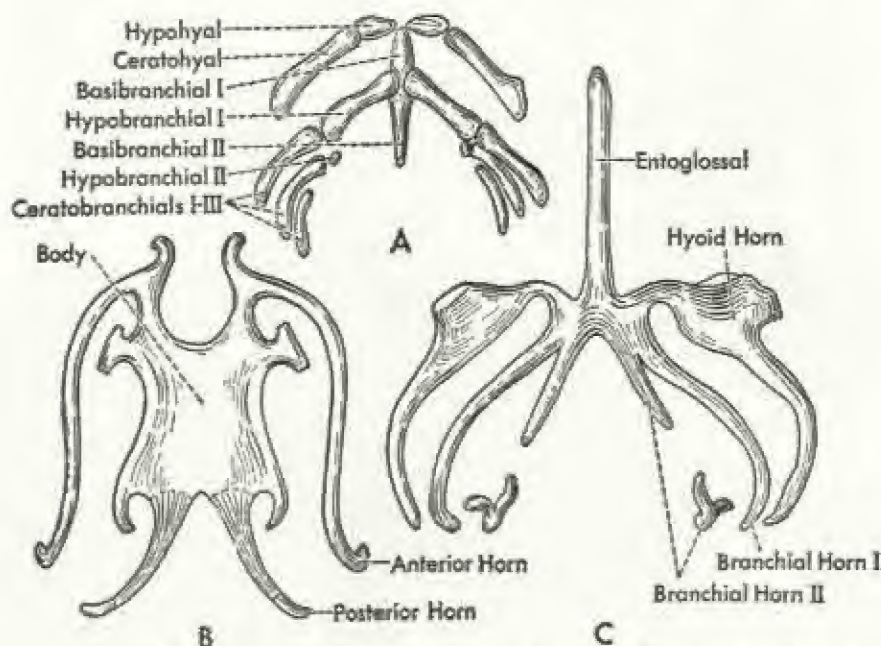


Fig. 493. Hyobranchial apparatus, ventral view. A, *Necturus*; B, frog, *Rana*; C, lizard, *Lacerta*. (A, after Hille; C, after Wiedersheim.)

(Fig. 499) with the squamosal, which covers the dorsal part of the quadrate, slightly more dorsal than the others. Mammals lack quadratojugals. The squamosal, probably homologous with one of the bones of the fish operculum, finally becomes the bone with which the lower jaw articulates in mammals.

The investing bones of the ventral surface of the skulls of lower vertebrates are *premaxillaries*, *palatines*, *pterygoids* (endopterygoids), *transpalatines* (ectopterygoids), and an unpaired *parasphenoid*. The parasphenoid,

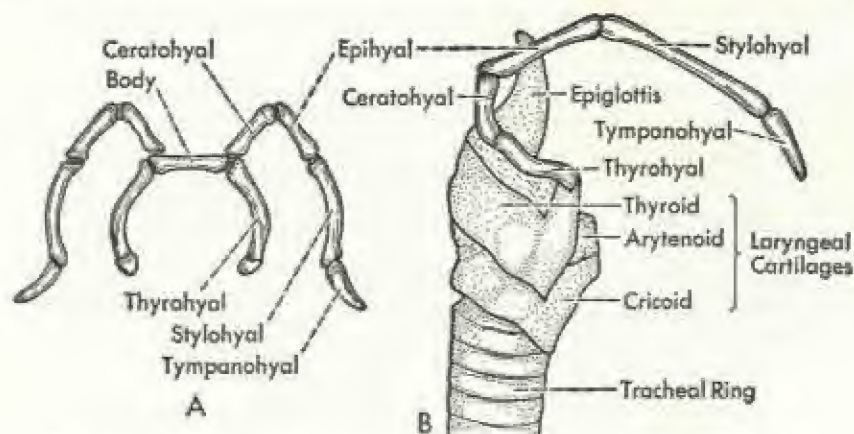


Fig. 494. Hyoid, larynx, and trachea of the cat. A, hyoid, dorsal view; B, left-side view. (After Reighard and Jennings.)

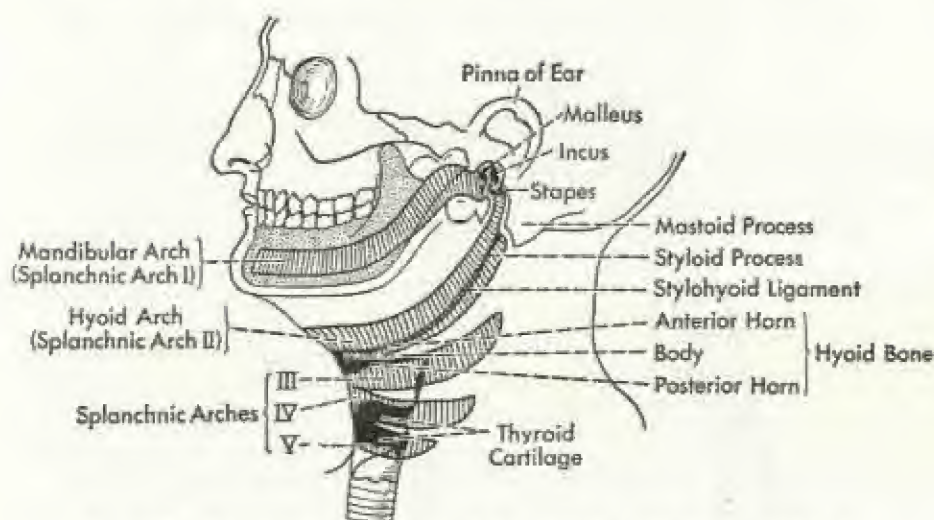


Fig. 495. Diagram to show fate of the ancestral splanchnic arches in man. The arches are represented by the areas shaded with parallel lines; the parts of them which persist in adult man are shown in black. (After Wiedersheim.)

usually closely applied to the cartilage of the ventral side of the neurocranium, is well developed in most fishes (Fig. 491) and amphibians but fuses with the anterior end of the basisphenoid in reptiles and birds. In mammals the anterior end of the parasphenoid becomes the *vomer* (Fig. 500), a bone of the ventral part of the nasal septum, while the posterior end may form part of the pterygoid region. Prevomers, found in all tetrapods

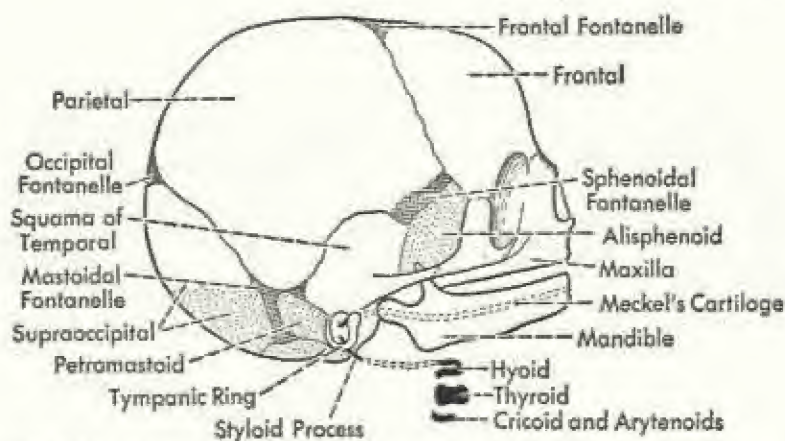


Fig. 496. A fetal human skull. Derivatives of the splanchnocranium are shown in black; investing bones, unshaded; replacing bones, dotted; fontanelles, crosshatched. (After Arey.)

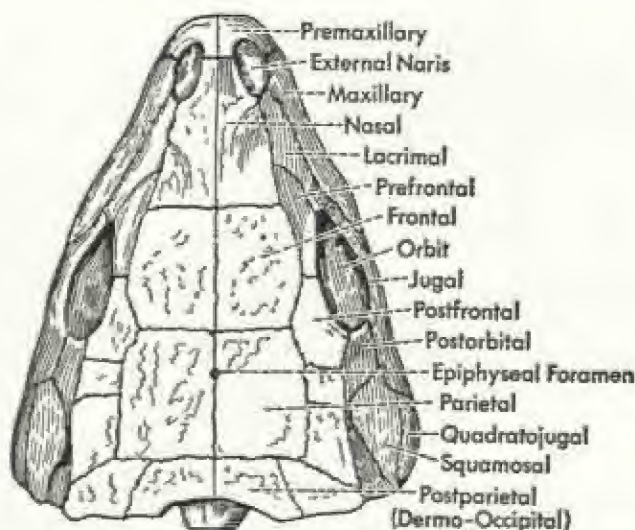


Fig. 497. Dorsal view of skull of a cotylosaur, *Seymouria* (*Conodectes*). (After Williston.)

except mammals, fuse into a single median bone in turtles and most birds. Primarily the palatines, pterygoids, and transpalatines are associated with the median side of the pterygoquadrate.

When the anterior ends of the digestive and respiratory passages become separated by the palate, support for this horizontal partition is provided by four pairs of bones: premaxillaries, maxillaries, palatines, and pterygoids.

The premaxillaries and maxillaries, while still retaining their duties as tooth-bearing upper jaw elements, send out horizontal palatine processes which meet in the mid-line to form the anterior part of the *hard palate*, or secondary roof of the mouth. The posterior part of this region is supported by both palatines and pterygoids in reptiles but by the palatines alone in mammals. In birds these parts remain so narrow that they fail to join into a hard palate.

The *investing bones covering over Meckel's cartilage* vary in number from nine pairs in some *Stegocephalia* down to the one pair of *dentaries* which make up the entire lower jaw of mammals. In the alligator (Fig. 492) five pairs are present, *angulars*, *supraangulars*, *splenials*, and *coronoids* in addition to the tooth-bearing *dentary*. It will be remembered that the articular bone, also present in the alligator's lower jaw, is of the replacing type. It is probable that in mammals the angular bone, which does not contribute to the formation of the lower jaw, becomes the *external tympanic bone* which forms the wall of the inner part of the external ear canal and supports the *external tympanic membrane*, popularly known as the "ear drum."

The comparative anatomy of the principal skull bones is summarized in Table VIII.

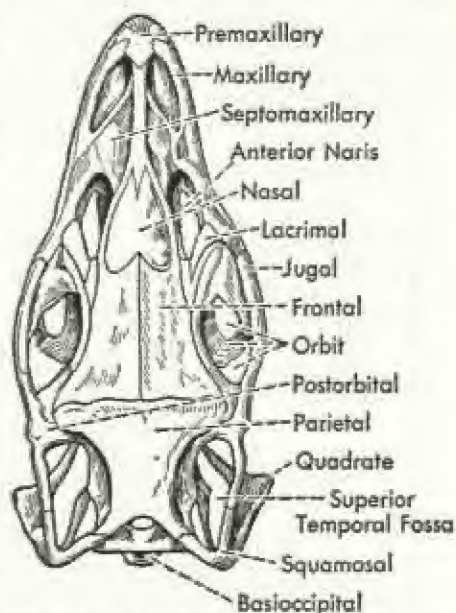


Fig. 498. Dorsal view of skull of *Varanus*, a lizard. (After Reynolds.)

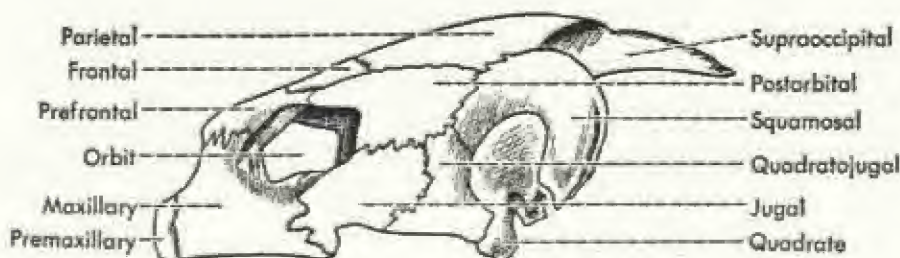


Fig. 499. Left-lateral view of skull of a turtle. (After Sayles.)

TABLE VIII. The Principal Bones of the Skull

Regions of Skull	Names of Bones	Replacing or Investing	Paired or Unpaired	Ganoid Fishes	Stegoccephalia	Urochela	Anura	Cotylosaurus	Sphenodon	Chelonis	Squamata	Crocodylia	Therapsids	Aves	Mammalia
Occipital Ring	Supraoccipital	R	U	-	1	-	-	+	+	+	+	+	+	+	+
	Exoccipital	R	P	+	+	+	+	+	+	+	+	+	+	+	+
	Basioccipital	R	U	+	1	-	-	+	+	+	+	+	+	+	+
	Basisphenoid	R	U	?	+	-	-	+	+	+	+	+	+	+	+
	Presphenoid	R	U												
Ventral Trough	Orbitosphenoid	R	P	+	2	+	2	2	4	-	4	-	+	+	+
	Mesethmoid	R	U												
	Prevacine	I	P	+	+	+	+	+	+	+7	+	+	+	+7	-
	Palatine	I	P	+	+	-	+	+	+	+	+	+	+	+	+
	Transpalatine	I	P	+	+	-	-	+	+	-	+	+	+	-	-
	Pterygoid	I	P	+	+	+	+	+	+	+	+	+	+	+	+2
	Parasphenoid	I	U	+	+	+	+	4	4	4	4	4	4	4	•
Otic Capsule	Opisthotic	R	P	+	1	-3	-	+	+	+	4	4	4	+	•
	Prootic	R	P	+	+	+	+	+	+	+	+	+	+	+	•
	Epiotic	R	P	+	+	+	+	+	+	+	+	+	+	+	•
	Epithelmid	R	P												•
Olfactory Capsule		R	P												
Pterygoquadrate (Upper	Quadrate	R	P	+	+	+	+	+	+	+	+	+	+	+	+
	Epityergoid	R	P	-	-	-	-	+	+	5	5	-	+	-	•
	Squamosal	I	P	?	+	+	+	+	+	+	+	+	+	+	+
	Quadrangular	I	P	?	+	-	+	+	+	+	-	+	5	+	-

Vomer and ?

Petrosal

Incus

Alisphenoid

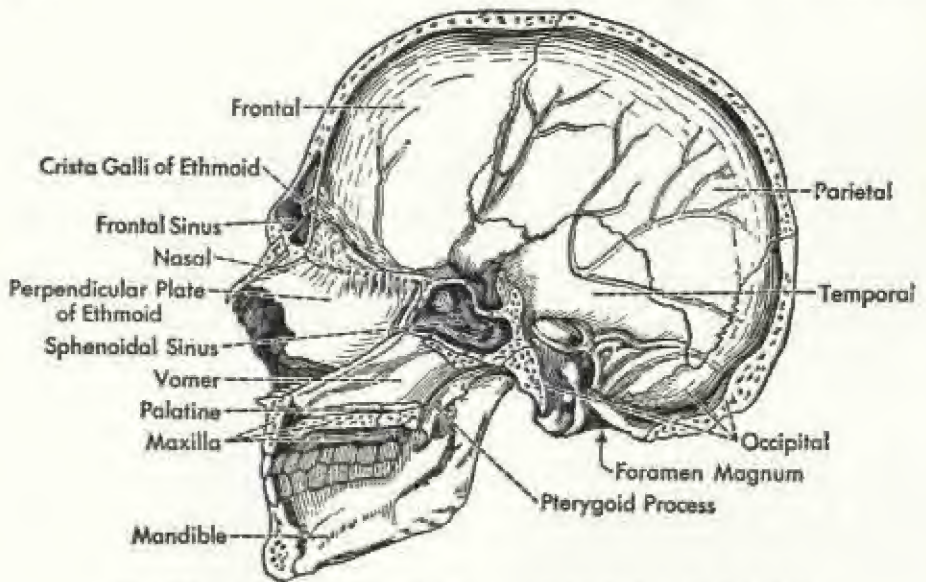


Fig. 500. Median section of a human skull. (After Spalteholz.)

5. Middle Ear Ossicles

The evolutionary history from the cartilaginous jaws of the dogfish to the middle ear ossicles of mammals is quite as remarkable as that of the aortic loops or the urogenital ducts. Primarily in *gnathostomes*, or vertebrates with jaws, the articular region of the cartilaginous lower jaw forms a movable hinge-joint with the quadrate region of the cartilaginous upper jaw (Fig. 489). A hyomandibular, extending from the angle of the jaws to the otic region, acts as the suspensorium of the jaws.

With the appearance of bone in the Osteichthyes these three key regions ossify as the articular, quadrate, and hyomandibular bones.

In the autostylic tetrapods the hyomandibular, no longer used to attach the jaws to the neurocranium, is reduced in size and enclosed in the middle ear cavity. In amphibians, reptiles (Fig. 694), and birds it forms the *columella auris* which transmits vibrations from the tympanic membrane to the internal ear.

In mammals additional modifications take place. Two investing bones, the dentary of the lower jaw and the squamosal of the upper jaw, provide the joint between these regions. The articular and quadrate, in reduced form, then move into the middle ear cavity to become reacquainted with their old associate the hyomandibular, or at least its homologue. The articular becomes the *malleus*, or *hammer*, and the quadrate becomes the *incus*,

or *anvil*, while the hyomandibular gives rise to the *stapes*, or *stirrup*, which is therefore the homologue of part or all of the columella of other tetrapods. There is thus established a chain of three bones (Fig. 488): the malleus, the "handle" of which lies against the external tympanic membrane, articulates with the incus which in turn articulates with the stapes. The last-named fits into the "oval window," an opening leading into the cavity of the internal ear. It is noteworthy that in mammals these parts are arranged in exactly the same order as their selachian homologues, namely, articular of lower jaw, quadrate of upper jaw, hyomandibular, and otic capsule.

6. Temporal Fossae

In the primitive Osteichthyes, Stegocephalia, and cotylosaurs (Fig. 497) the investing roof of the skull has five openings: a pair of external nares, a pair of orbits, and a single median small pineal foramen. Behind the orbits the roof is complete and encloses a large *temporal space* on either side of the brain case. Large jaw muscles occupy much of this space in the intact animal. These skulls, in which the posterior part of the roof is complete, exhibit what is known as the **ANAPSID** (*an*, without; *apsid*, arch, loop) condition.

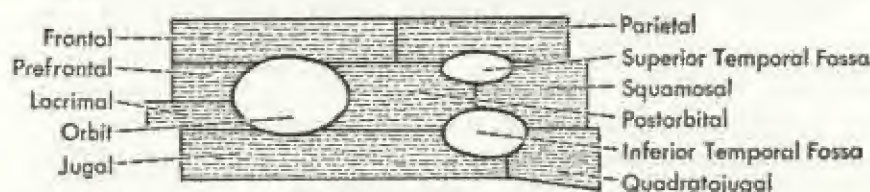


Fig. 501. Schematic plan to show relationship of temporal fossae to neighboring bones on left side of skull.

In some reptiles two additional pairs of openings, in the posterior part of the roof, are present (Fig. 501). The more dorsal *superior temporal fossa* is usually bounded by the parietal, squamosal, and postorbital. Ventral to this opening is the *inferior temporal fossa* which is usually surrounded by postorbital, squamosal, quadratojugal, and jugal. This **DIAPSID** type is found in Rhynchocephalia (Fig. 490), Crocodilia, pterosaurs, dinosaurs and related groups believed ancestral to birds. Birds have a modified diapsid type of skull.

In therapsid reptiles only the inferior temporal fossa is present. This **SYNAPSID** condition is also found, in modified form, in mammals and some of the higher therapsids in which the fossa extends as far dorsally as the parietal. When the postorbital disappears, the fossa becomes continuous with the orbit.

Lizards and possibly some other reptiles have what appears to be only the superior temporal fossa, the PARAPSID condition, although there is still considerable doubt concerning the relationships of the parts of the skull in these animals.

Turtles (Fig. 499) are anapsid but they are believed to have acquired this condition secondarily as a result of the filling in of the fossae by enlargement of the individual bones.

7. Vertebrate Skulls

(a) **Cyclostomes.**—The skull of cyclostomes (Fig. 502) is quite aberrant from that of other vertebrates. In the embryonic "ammocoetes stage" of *Petromyzon*, the parachordalia and trabeculae of the brain-case floor are evident and normal, as well as the otic capsules that surround the ears, but a cartilaginous envelope does not entirely surround the brain, since the roof of the brain case is completed in fibrous connective tissue, while the absence of

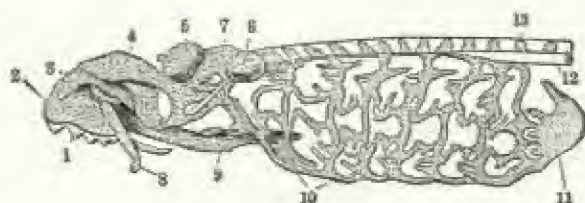


Fig. 502. Lateral view of skull of *Petromyzon*. 1, horny teeth; 2, annular cartilage; 3, anterior labial cartilage; 4, posterior labial cartilage; 5, nasal capsule; 6, auditory capsule; 7, dorsal portion of trabeculae; 8, lateral distal labial cartilage; 9, lingual cartilage; 10, branchial basket; 11, cartilaginous cup supporting pericardium; 12, sheath of notochord; 13, anterior neural arches, fused together. (From Shipley and MacBride, after Parker.)

jaws entirely changes the character of the anterior part of the skull. The skeletal structures of the large tongue may possibly be homologous with the lower jaws of fishes. At any rate the tongue bears rasping epidermal teeth and is bilateral in origin like the lower jaws. The cartilaginous elements which lie anterior to the tongue and support the jawless mouth seem to be peculiar to cyclostomes. They are obviously necessary adaptations on account of the suctorial and parasitic habits of these animals. The posterior part of the cranium, which ends abruptly with the otic capsules, is without any true occipital region.

Since in higher vertebrates the occipital region is to be regarded as a derivative from the anterior vertebrae of the spinal column, as the relation

of the cranial nerves indicates, it could hardly be expected to be developed in animals whose skeletal axis has not yet emerged from the notochordal stage.

The skeletal support for the gills in cyclostomes is a continuous grillwork of cartilage, more external in position than the splanchnocranium of other fishes and not homologous with it.

(b) **Elasmobranchs.**—The typical cartilaginous skull of elasmobranchs furnishes a morphological point of departure for the skulls of all other vertebrates (Figs. 231 and 474). In these primitive fishes the neurocranium is a continuous protective brain case. It is the result of the fusion of embryonic cartilaginous elements, as already described, which may be partially calcified in some adults. The splanchnocranium is present in its most perfected form, being nowhere fused or incorporated with the neurocranium. The first arch of the splanchnocranium serves as both upper and lower jaws and is abundantly supplied with integumental teeth. Perhaps the feature most peculiar to the elasmobranch skull, and least copied by subsequent forms, is the development of a snout in the form of *rostral cartilages* that project anteriorly, thus making the mouth ventral in position. In the elasmobranch *Pristis* (Fig. 20c), the extended rostrum is supplied on either lateral margin with sharp teeth, which give it the name of "sawfish."

(c) **Ganoids.**—The transition from a single cartilaginous skull to a double skull is effected in this group, which characterizes it as a connecting link between the lower fishes and the higher vertebrates. While an inner cartilaginous capsule is retained unossified around the brain in the cartilaginous ganoids (Chondrostei), there is added to the outside of it a bony skull of many parts, derived from dermal scales (Fig. 476). The bones in the skulls of cartilaginous ganoids are all of the investing type, and since they are very numerous, their homology with the individual investing bones in the skulls of higher forms is doubtful. The number of elements in the splanchnocranium is reduced somewhat as compared with that of elasmobranchs.

The skulls of bony ganoids (Holostei) have two sets of bone, investing on the outside and replacing on the inside, the latter ossified from the cartilaginous brain case. Much cartilage still remains, however, after the replacing bones appear.

(d) **Teleosts.**—Bony fishes exhibit a great variety of skulls, all referable more or less directly to the type characteristic of bony ganoids. In the lower teleosts considerable cartilage persists unossified, but in most cases the name "teleost" (*tele*, entire; *ost*, bone) is justified (Fig. 491). No other vertebrates have as many bones as teleosts.

(e) **Stegocephals.**—The problematical extinct Stegocephalia, some of which had skulls over three feet in length, show a large number of bones, probably investing in character, forming an extensive roof over a cranium of very small capacity. For the most part these bones fit closely together, allowing only for restricted orbital and nasal cavities, and suggesting the skull of ganoids rather than that of the amphibian type. The fact that cartilages are missing in fossils leaves much to be desired in working out homologies. Between the parietal plates on the top of the skull is an *interparietal foramen*, the window through which a third *epiphyseal eye* probably looked upward. There was an abundant occasion for these lowly monsters to look upward, at least in an evolutionary sense.

(f) **Modern Amphibians.**—Modern amphibians are characterized by much less cartilage in the skull and also by fewer bones than are found in skulls of the bony fishes. It is quite reasonable to suppose that they represent a separate, divergent, evolutionary line, distinct from those of other tetrapods and of teleosts, although all may be referred to a common origin in primitive bony fishes.

The restricted cranium itself, that houses the brain, is somewhat tubular and elongated, extending far anterior between the eyes without any inter-orbital septum. The conspicuous width of the skull, as well as the extensive horizontal mouth-opening, is largely due to outrigger bones which form the upper jaw and connect with the widened ethmoidal and otic regions. Of the few replacing bones the exoccipitals, bearing the two condyles and the prootics which make up the major part of the otic capsules, are the most constant. There are no basi- or supraoccipitals, but the place of the latter is taken by a band of connective tissue, or a narrow cartilage, the *tectum synoticum*, which joins the two otic capsules together by a dorsal bar (Fig. 475).

Urodeles show a greater parsimony of inner cartilaginous skull than the anurans, since the embryonic trabeculae never meet and fuse, thus leaving this region of the skull, as in the adult *Necturus*, without a cartilaginous floor. The quadrate and pterygoid are continuous, while the quadratojugal fuses with the squamosal. The parasphenoid of urodeles is a large flat investing bone, sometimes bearing teeth, covering nearly the entire floor of the skull, whereas in anurans it is reduced to a peculiar T-shaped structure with the shaft pointing anteriorly (Fig. 503). The parietals and frontals also, which are separate in urodeles, become incorporated into *parieto-frontals* in anurans, and still other hyphenated bones mark the progressive simplification of the amphibian skull.

Little of the original cartilage remains in the skull of the legless caecilians

(gymnophiona), but there is more fusion of the investing bones than in caudates, making a compact skull adapted to the subterranean life of these curious aberrant animals.

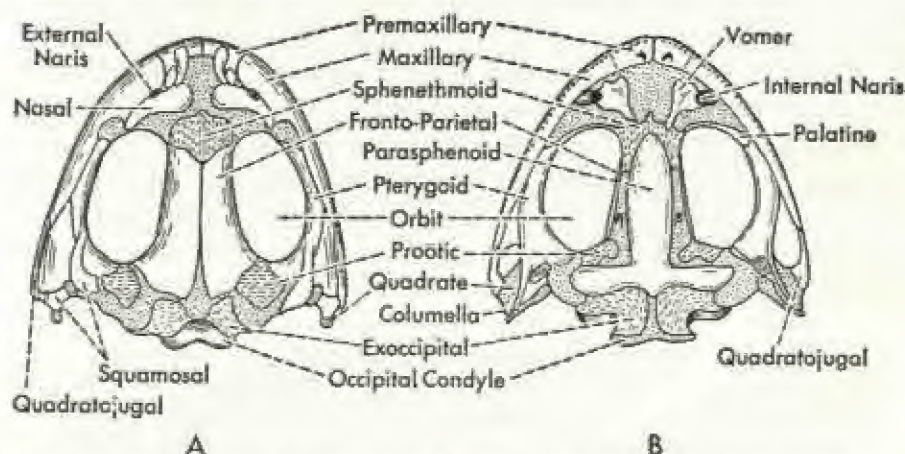


Fig. 503. Skull of a frog, *Rana*. A, dorsal view; B, ventral view. (After Reynolds.)

(g) **Reptiles.**—Cartilage largely disappears from the adult reptilian skull, persisting in *Sphenodon* and in lizards to a greater extent than in other modern reptiles. Investing bones are more numerous than in amphibians while replacing bones are many and usually independent or unfused.

Except in snakes, the *interorbital septum* separates the two orbits of the eyes, in consequence of which the brain does not extend as far anteriorly as in amphibians. Between the pterygoid and the maxillary an additional bone, the *transverse* or *ectopterygoid*, is added, greatly strengthening the jaw. Premaxillaries, which are usually united in adult reptiles, are embryonically double, and the same is true of the parietals. Meckel's cartilage is surrounded by a full complement of investing bones (Fig. 492).

In turtles a false roof to the skull, formed by expanded postorbitals, parietals, and squamosals, reminds one of the stegocephals, for the entire chelonian skull is exceptionally large in comparison to the size of the enclosed brain (Fig. 481). A single median vomer and the parietals, which remain separate, are present, but several bones that might be expected, such as the nasals, ectopterygoids, and lacrimals, are absent in turtles.

The jaws of snakes are a distinctive feature, since they are capable of great distension, enabling these animals without the aid of hands to swallow their relatively large prey whole. The two parts of the lower jaw are not only loosely joined to the cranium on either side by the movable quadrates, but

are also anteriorly united at their distal ends by an elastic ligament, permitting their lateral separation to a considerable extent. Each half of the upper jaw region consists of a movable chain of four bones, namely: quadrate, pterygoid, palatine, and maxillary. The quadrate is attached to the posterior part of the brain case in a hinge-joint, while the maxillary is attached anteriorly in the same fashion. The pterygoid and palatine do not form a rigid hard palate but are moved as the ventral free end of the quadrate is swung back and forth. Through them the movements of the quadrate are imparted to the maxillary. At the same time the lower jaw, which articulates with the ventral end of the quadrate, is also moved back and forth. With each backward movement of the jaws the teeth, which are tipped posteriorly, hook into the prey and draw it down the throat.

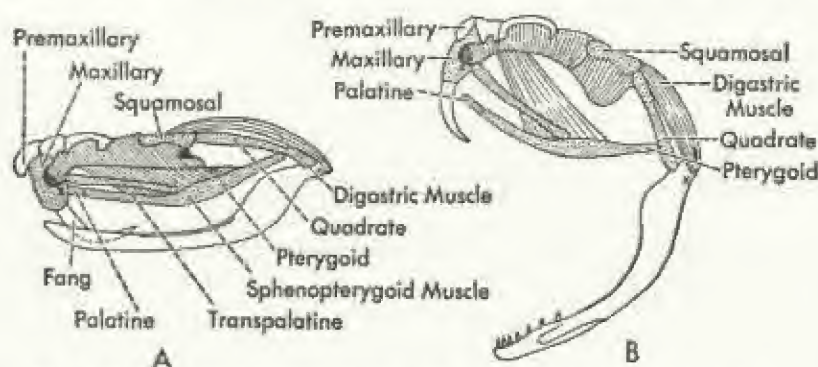


Fig. 504. Jaw mechanism of the rattlesnake. A, with mouth closed; B, with mouth open. By a contraction of the digastric muscle the mouth is opened; at the same time another muscle draws the entire upper jaw, hinged on the quadrate and maxillary, forward; in this manner the fang is swung out into striking position. (After Hiltzheimer.)

In poisonous snakes each fang is set in a socket in the corresponding maxillary. As the snake prepares to strike, it opens its mouth and moves the chain of upper jaw bones forward, thus swinging the fang out into striking position (Fig. 504). By moving the upper jaw elements posteriorly the snake returns its fangs to the resting position within the mouth cavity.

In crocodiles and lizards the two parts of the lower jaw are joined in front by sutures, but in turtles they are fused into one solid mandible. The formation of an extensive hard palate, in which the maxillae, palatines, and pterygoids all take part, in the case of alligators and crocodiles causes the posterior opening of the *choana* on either side to be pushed back so far down the throat that these animals are able to drown their prey without being drowned themselves. This feat is accomplished by the aid of a curtain-like

velum that shuts off the posterior openings of the nostrils (choanae) from the surrounding water, thus enabling the reptile to breathe through the choanal passage-way with the tip of the snout out of water, while the mouth is kept submerged until the struggling prey within, held fast by the conical teeth, is drowned (Fig. 350).

(h) **Birds.**—In birds the most characteristic feature of the skull, like that of the entire skeleton, is the elimination of every bit of bone that can be spared (Fig. 505). Compared with reptiles, from which birds arose, a typical avian skull is more spherical and roomier. The relatively enormous size of the eyes, together with the well-developed interorbital septum, tends to restrict the brain to the posterior part, while the ear-capsules on either side are more deeply embedded than in reptilian skulls.

Notwithstanding the fact that many typical bones, both replacing and investing, are distinguishable in the embryo, they become welded together in the adult by the early closure of the sutures into an almost continuous capsule of bone, which is remarkably strong and protective in spite of its lightness and the paucity of bony material employed.

The *zygomatic arch* is reduced to a slender bar, the *postfrontals* disappear, and the *premaxillaries*, *maxillaries*, *palatines*, and *pterygoids* are so narrowed that they fail to join into a hard palate. The lightness of the skull is furthermore enhanced by the pneumaticity of the bones, characteristic of the entire skeleton, and also by the substitution of a horny beak in place of heavy teeth set in the jaws. Only in the interorbital septum and in the ethmoid region does cartilage persist.

Remains of the investing parasphenoid fuse with the replacing basisphenoid to form a unique, forward-projecting *sphenoidal rostrum* along the floor of the cranium. The single occipital condyle on the basioccipital bone is similar to that in reptiles, allowing great freedom of movement to the

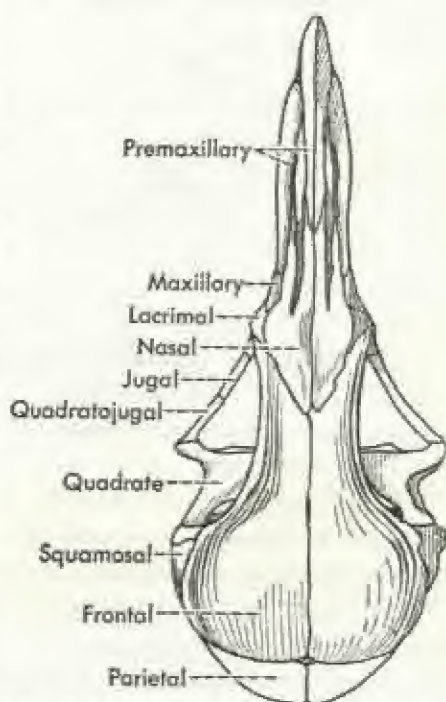


Fig. 505. Dorsal view of skull of a pigeon, *Columba*. (After Heilmann.)

bird's head. With the rotation forward of the condyle, along with the shift in position of the foramen magnum, these two landmarks appear at the ventral base of the skull instead of at the posterior aspect of it. This change, which is associated with the semi-erect posture of birds, modifies the manner in which the skull is carried by the vertebral column.



Fig. 506. Diagram to show the movable upper jaw of a parrot. (After Boas.)

The quadrate has a freely movable articulation with the skull, so that the lower jaw has a double joint with the skull as in the lizards and snakes. Many birds have a movable joint between the upper jaw and the skull which enables them to raise the upper jaw without at the same time carrying the cranium with it (Fig. 506), an unusual performance for a vertebrate. The curious hyoid apparatus of the woodpeckers (Fig. 236) exhibits another peculiar modification of the bird's skull in connection with the mechanical withdrawal of the extended tongue.

The orbits of the eyes are close together, separated only by a thin septum without any intervening part of the brain between them. It is difficult to imagine how monstrous a human skull would be if, like that of a bird, each orbit were as capacious as the entire cranial cavity.

(i) **Mammals, with special reference to man.**—The skull bones of the primitive monotremes are highly specialized on account of their beaklike mouth parts and the early fusion of bones which obliterates the outlines of the component parts.

It may be said of the mammalian skull in general that the splanchnocranium becomes more completely incorporated with the neurocranium than in any other class of vertebrates. With the process of cranial expansion to accommodate the increasing size of the brain, there is a shortening of the jaws, while the retreating face bones become more and more overshadowed by the upward-bulging cranium until, in primates at least, they are ventral to the cranium in position rather than anterior to it. This evolutionary tendency is made clear when one compares the skull of a deer with that of a man (Fig. 507).

Although there is considerable fusion of bones in the mammalian skull, the sutures usually remain quite distinct, except in old age when they are apt to become obliterated. When of the zig-zag type (Fig. 423), formed by the dove-tailing of the bones together edge to edge, the sutures make an interlocking joint almost as firm as solid bone.

In man, with the assumption of erect posture associated with the bipedal habit, the foramen magnum and surfaces for articulation with the first vertebra have shifted to a position beneath the skull instead of at the posterior

end (Fig. 507). The human orbits have also migrated forward to positions close together on either side of the nasal region where both eyes may be directed forward, thus permitting binocular vision. Yet as far as the actual bones are concerned the human skull is built according to the same general plan as are the skulls of most mammals. In man, however, more than in most other mammals, groups of embryonic bones tend to fuse together to form bone complexes. The total number of separate bones in the adult skull is thus reduced to 22 plus the 3 pairs of middle ear bones already described.

The OCCIPITAL (Figs. 487 and 500) is laid down as five separate parts. Four of these make up the replacing ring around the foramen magnum composed of the *basioccipital*, the two *exoccipitals*, and the ventral part of the *supraoccipital*. The fifth is the investing dorsal half of the supraoccipital which sometimes remains separate as the *interparietal*, a condition commonly found in other mammals. In man it is also known as the *Inca bone* (Fig. 508) for the reason that it has been often found in the skulls of the aboriginal Incas of Peru. The suture of *Mendoza* (Fig. 509), between

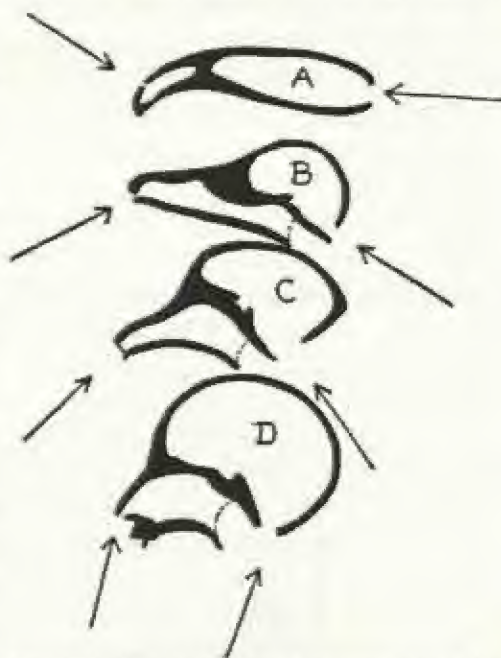


Fig. 507. Sagittal diagrams through the skulls of, A, a salamander; B, deer; C, baboon; and D, man. (The arrows indicate an evolutionary change in the relation of the external nose-opening and the foramen magnum.) (Modified from Wiedersheim.)

the two parts of the human supraoccipital, ordinarily disappears about the third fetal month. The other parts fuse between the fourth and sixth years. By the twenty-fifth year the occipital unites with the sphenoid bone at their basal regions, their only point of contact. On the exoccipital portions, alongside the foramen magnum, is a pair of *occipital condyles* which articulate with the atlas.

The SPHENOID bone, the base of which is immediately anterior to the basioccipital region, is made up of at least eight embryonic parts. The *basisphenoid* and the *presphenoid* form the median *body* of the bone. The two *alisphenoids* become the *great wings* (Fig. 487) while the two *orbitosphe-*

noids become the *small wings*. The two investing *pterygoids* attach to the regions of junction of the body and the great wings as the *pterygoid processes*. All of these parts have fused together by the end of the first year. On the inner surface of the basisphenoid portion there is a deep depression, the *sella turcica* or "Turk's Saddle," which is a conspicuous landmark on the inside of the mammalian skull and in which is cradled the downward-projecting *hypophysis* of the brain. Just anterior to the *sella turcica* there is a transverse groove in which lies the *optic chiasma* where fibers of the optic nerves cross from one side to the other. Enclosed within the body of the sphenoid is a pair of *sphenoidal air sinuses* (Fig. 500), separated from one another by a bony septum. Each opens into the postero-dorsal part of the corresponding nasal cavity.

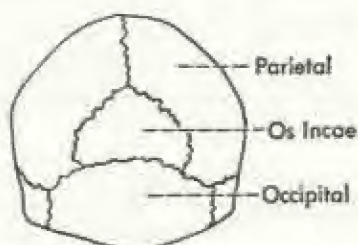


Fig. 508. Diagram of the back of a skull, showing the presence of the *Inca bone*. (After Wiedersheim.)

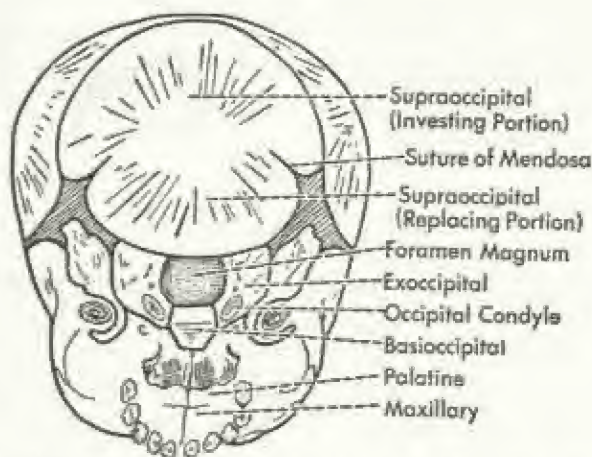


Fig. 509. The base of an infant's skull before the fusion of the occipital bones. The *suture of Mendosa* separates the investing and replacing portions of the supraoccipital.

The **ETHMOID**, a thin delicate bone lying in front of the sphenoid, forms the dorsal part of the nasal septum as well as portions of the lateral walls of the nasal cavities (Figs. 469, 487, and 500). It is composed of three replacing bones, a *mesethmoid* and two *ectethmoids*, which unite about the twelfth to fifteenth month. The *mesethmoid* is composed of (1) the *perpendicular plate*, part of the nasal septum, (2) the *crista galli*, an upward

projection into the brain cavity in the same plane as the perpendicular plate, and (3) a portion of the *cribriform plate*, which lies at right angles to the other two parts and forms a part of the roof of the nasal cavities. The cribriform plate (*cribrum*, sieve) is so called because it is perforated like the top of a pepper-box for the passage of the brushlike olfactory nerves, growing back from the patches of sensory epithelium in the nasal chambers. The multiplicity of foramina for the olfactory nerves is peculiarly mammalian, although in *Ornithorhynchus* there is only a single pair of olfactory foramina while the Cetacea, which have apparently entirely lost the sense of smell, have no cribriform perforations. Each ectethmoid contributes to the cribriform plate and makes up part of the wall between a nasal cavity and the corresponding orbit. It is composed of thin, spongy bone enclosing large cavities, *ethmoidal cells*, which open into the adjacent nasal cavity. These cells are sometimes known collectively as the *ethmoidal sinus*. Each of the ectethmoids gives rise to two *turbinals (conchae)* which extend diagonally down from its medial wall (Figs. 486 and 677).

THE VENTRAL NASAL CONCHAE, one of which is on the lateral wall of each nasal cavity ventral to the two ethmoidal conchae, ossify as separate bones in the lateral walls of the cartilaginous nasal capsules. They do not fuse with the other bones of the nasal wall. In many mammals there are elaborate turbinal bones, in some cases in the form of extensive, delicate scrolls almost filling the nasal cavities. They provide additional surface for warming and moistening air as it passes through on its way to the lungs, as well as providing for extra olfactory epithelium.

THE VOMER, or "ploughshare," a thin bone forming the postero-ventral part of the nasal septum (Fig. 500), lies between the ethmoid and sphenoid above and the hard palate below. This bone is homologous with the anterior end of the parasphenoid of lower vertebrates and not with their paired prevomers. The anterior part of the nasal septum remains cartilaginous.

THE PARIETALS, which form much of the dorsal and lateral walls of the brain case, are ordinarily separated throughout life by a *sagittal suture* from which has been derived the name *sagittal plane*, applied to the plane dividing a bilaterally symmetrical animal into right and left halves.

THE FRONTAL forms the forehead, anterior part of the cranial roof, roof of the orbits, and part of the roof of the nasal cavities. Until about the eighth year this bone consists of a pair of bones separated by the *metopic suture* (Fig. 510). In most mammals the two frontals remain separate throughout life. In the median part of the frontal bone is a pair of *frontal sinuses* (Figs. 500 and 511), separated by a bony septum, which communicate with the nasal cavities immediately ventral to them. Bony out-

growths of the frontal bones give rise to the paired horns of ungulates as described in Chapter X.

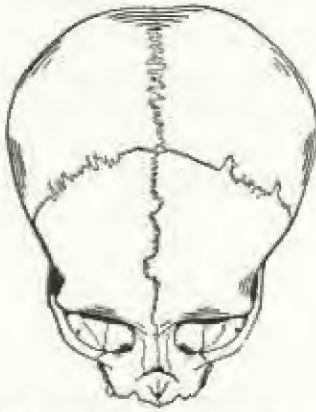


Fig. 510. The skull of a young boy, showing the *metopic suture* separating the two parts of the frontal bone.

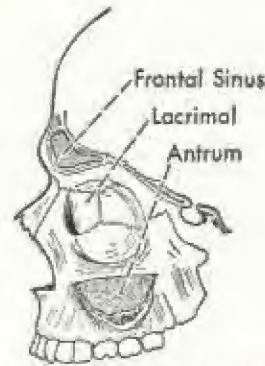


Fig. 511. Left-side view of facial part of human skull, with part of upper jaw cut away to show *antrum of Highmore* and part of frontal removed to show *frontal sinus*.

The **NASALS**, lying in the anterior part of the roof of the nasal cavity, support the bridge of the nose, the shape of which is determined largely by the size and shape of these bones (Figs. 469, 512, and 513).

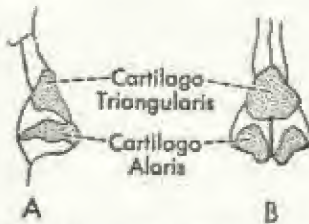


Fig. 512. The flexible cartilaginous elements (dotted) of the projecting part of the human nose. A, side view from the right; B, front view. (After Gegenbaur.)



Fig. 513. "The external nose varies strikingly in the styles of its architecture." (After Gallup.)

Each of the **LACRIMALS** (Fig. 511) forms part of the medial wall of the orbit anterior to the ethmoid. The anterior part of the bone bears a vertical *lacrimal groove* through which the *lacrimal (tear) duct* leads into the nasal cavity. Mammalian lacrimals may be homologous with the prefrontals of

reptiles which they resemble more than they do the so-called "lacrimals" of the latter.

The MAXILLAE, which are the largest of the face bones in man, not only bear teeth and serve as upper jaws, but they also extend inward, forming a part of the hard palate in the roof of the mouth. Each is hollowed out by a large irregular sinus, the *antrum of Highmore* (Fig. 511), which communicates with the nasal cavity. Into the ventral side of the antrum project the bony capsules which surround the roots of at least the first two molar teeth. If the sinus is particularly large, all five molariform teeth, and even the incisors, may be represented here. Occasionally the actual roots of the teeth may be exposed in the cavity. Like all the other air sinuses of the skull, the antrum is lined with mucous membrane and in the case of man is one of the happy hunting grounds of bacteria.

Each maxilla is composed of a small *premaxillary*, into which the incisor teeth are set, and a *maxillary* bearing all of the other teeth. Premaxillaries are rudimentary or wanting in bats and some edentates. The premaxillaries and maxillaries are independent in most mammals, at least during early life. In man, however, the fusion occurs before birth.

The apparent absence of premaxillaries (or *intermaxillaries*, as they are sometimes designated) was formerly held to be a distinguishing skeletal mark of human kind. It is interesting to recall that the poet-biologist Goethe discovered their presence in man and wrote hilariously in 1784 to his friend Herder: "Nach Anleitung des Evangelii muss ich Dich aufs eiligste mit einem Glück bekannt machen, das mir zugestossen ist; Ich habe gefunden—weder Gold noch Silber, aber was mir unsägliche Freud macht, das *os intermaxillare* am Menschen." (According to the gospel method I must let you know in all haste of a lucky thing that has befallen me. I have discovered—not gold nor silver, but what gives me unspeakable joy, the *os intermaxillare* of man.)

The JUGALS (ZYGOMATICS OR MALARS of human anatomy) form the *zygomatic arches*, or "cheek bones," by connecting with processes from the squamosal parts of the temporals and from the maxillaries anteriorly (Figs. 469 and 496). Each contributes to the floor of the orbit.

The PALATINES (Fig. 509), lying immediately behind the maxillae, form the posterior part of the hard palate as well as sending processes into the walls of the orbits and the nasal cavities.

Each TEMPORAL (Fig. 496) consists of four regions, namely, the squama, the petromastoid, the tympanic ring, and the styloid process. The *squama*, or "scale," is the somewhat circular thin antero-dorsal part which corresponds with the squamosal of other mammals, in most of which it remains a

separate bone. On the squamosal is the *mandibular fossa* into which the condyle of the lower jaw fits. The *petromastoid*, or *petrosal*, postero-medial to the squama, is a thick region containing the internal ear and most of the middle ear cavity with its three auditory ossicles discussed in section 5. It is formed chiefly by the fusion of the three otic bones—*proötic*, *opisthotic*, and



Fig. 514. A section through the mastoid process, showing the spongy character of the bone.

epiotic—which are laid down in the original otic capsule. In the posterior part of the petromastoid are the *mastoid cells*, spaces which communicate, through a common passage-way, with the middle ear cavity (Fig. 514).

Included in the temporal assembly there are not only the otic bones, middle-ear bones, and squamosal, but also a ringlike fragment, the *tympanic ring*, surrounding the *external auditory canal* across the inner end of which the *tympanic membrane* is stretched. This small bony element is probably the homologue of the angular bone from the lower jaw of other vertebrates. Attached to the petromastoid medial to the external auditory canal is the *styloid process*, a remnant of the hyoid arch, which probably represents the tympanohyal, from the anterior horn of the hyoid arch of many mammals (Fig. 494).

During development flat skull bones grow out from centers of ossification, like spreading ripples from a pebble thrown into a quiet pond, with the result that when the advancing edges of three or more enlarging bones meet, a small unossified area is temporarily caught between them. Such an open area is called a *fontanelle*, so named by some imaginative pioneer of anatomy because the throbbing of the blood vessels faintly visible at such regions in the infant's skull suggested a "little fountain." In man at least six fontanelles, around the parietal bones, are present at birth (Fig. 496): first, a large diamond-shaped *frontal fontanelle* on the top of the head between the frontals and the parietals, which usually closes about the end of the second year; second, the *occipital fontanelle*, triangular in shape and lying between the occipital and the parietal bones, that closes at the end of a few months; third, a pair of small *sphenoidal fontanelles*, which are formed on either side of the skull by the union of the frontal, parietal, temporal, and sphenoidal bones; and fourth, the *mastoidal fontanelles*, likewise small and paired, that occupy the posterior space between the parietal, temporal, and occipital bones.

Sometimes tiny *sutural*, or *Wormian*, bones occur as extra elements between the usual bones. They are found most often in the *lambdoidal suture*, between supraoccipital and parietals, but may also occur in fontanelles.

In childbirth the fontanelles are doubtless an adaptation of great practical value, enabling the large-headed infant to emerge into the world through a comparatively narrow gateway, since the cranial bones, as yet sutureless, can temporarily slip past each other at the edges without injury to the soft brain within. Long ago Hippocrates pointed out that it is quite possible, if the head has become somewhat misshapen in the process of childbirth, to mold the cranium back into conventional contours without injury, almost as if the brain were clay in the potter's hands.

Certain primitive races, like the Flathead Indians of North America and the nobility among ancient Peruvians, seized upon this possibility of shaping the plastic skull of the newly-born infant in order to acquire a conspicuous and distinctive form of the head which, if not an improvement on nature, at least had the quality of lending to its possessor a mark that set him apart from ordinary people in a sort of plastic anatomical aristocracy of his own (Fig. 515).

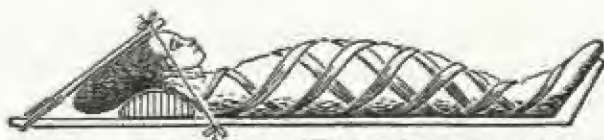


Fig. 515. Manner of skull deformation among ancient Peruvian Indians.

The late Dr. Louis R. Sullivan of the Department of Ethnology in the American Museum of Natural History in New York kindly gave permission to quote the following information concerning head deformation in North America. "The study of physical types is complicated by the widespread deformation of the head. In some cases it is unintentional, being produced by the hard pillows and cradleboards used. In many instances, however, the head has been intentionally deformed by mechanical devices. The two principal types of artificial deformation are the fronto-occipital flattening (Fig. 516) and the Aymara conical distortion (Fig. 517). There are various subtypes of each of these deformations. The custom was previously widespread, being recorded in one form and another from Africa, Malay, Philippines, France, Scandinavia, and Asia Minor. It is becoming less common in America at the present time. In some tribes the entire population practiced deformation while in others it was confined to one sex or even to the chiefs alone. Investigation has shown that it does not affect the mental ability of the subject and that it is not transmitted."

On account of the increasing size of the mammalian brain several of the cranial bones shift from their original position. This is particularly true of the cetacean skull, where the parietal bones are divorced from each other



Fig. 516. Fronto-occipital flattening of the skull of a north-west coast Indian. (Outline from photograph T/22177, Amer. Mus. of Nat. Hist.)



Fig. 517. Aymara or conical deformation due to bandages, Peruvian Indian. (Outline from photograph 99/3515, Amer. Mus. of Nat. Hist.)

and shoved over to an extreme lateral position (Fig. 518), while the supraoccipital extends forward between them even as far as the frontals, making up most of the roof of the skull. The maxillaries, meanwhile, push back posteriorly and form a considerable part of the cranium, invading the territory ordinarily occupied by the frontals, which now become squeezed narrowly between the backward-extending maxillae and the forward-pushing supraoccipital.

The MANDIBLE, or lower jaw, is formed by the union of two tooth-bearing dentary bones. It bears a pair of *condyles* which articulate with the

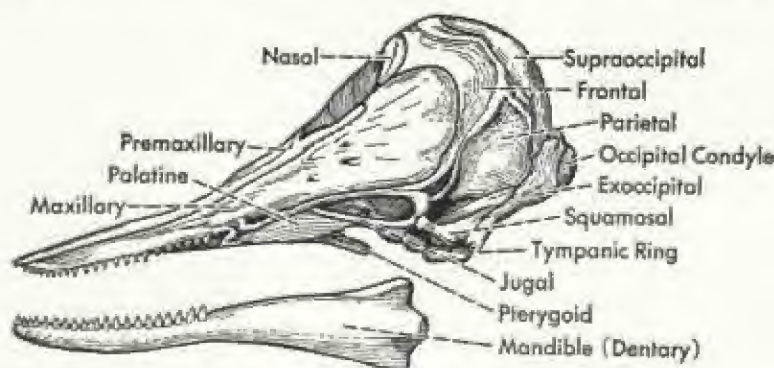


Fig. 518. Skull of a dolphin, in which the bones of the cranium are much modified. [After Schimkewitch.]

mandibular fossae of the temporal bones. Although in most mammals the two sides are separate they fuse into one solid piece in bats, perissodactyls, and primates.

Since long before the time when Samson slew a thousand Philistines with the jawbone of an ass, the mandible has in many ways been an outstanding bone of interest. Except for the tiny middle ear ossicles, it is the

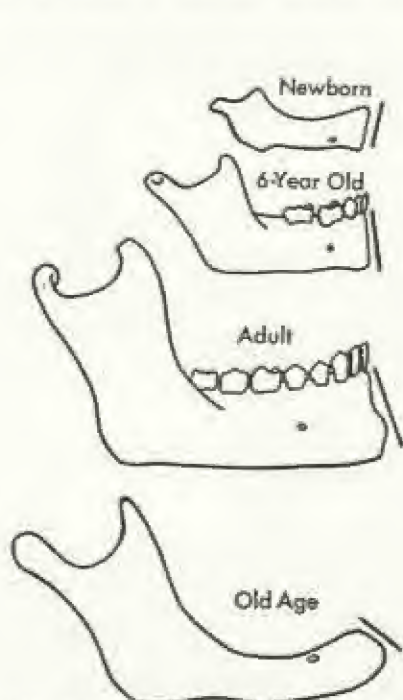


Fig. 519. Changes in the chin-angle during the life of the individual. (Ontogeny.) Compare with Figure 520.



Fig. 520. Changes in the chin-angle during the history of the race. (Phylogeny.) Compare with Figure 519.

only mammalian skull bone that has an independent movement of its own. In man it has gone a long way, in adjustment to changing conditions, from its cartilaginous prototype still surviving in the dogfish. At no time in its history has there been any cessation in function, although upright posture and the resulting liberation of the hands, together with the effeminate modern days of soft cooked food, have made it no longer imperative for the jawbone to serve as a nutcracker and bonecruncher. In some monkeys and apes the lower jaw may make up as much as forty per cent of the total weight of the skull, but in modern man it falls to less than fifteen per cent.

There is no doubt that its golden age of efficiency is past and now it is turned to other uses. Instead of being employed as a means of terrifying enemies by the frightful gnashing of bared teeth, it has become a part of the skeletal framework for the display of smiling friendliness and persuasive diplomacy.

In the infant before the teeth have forced the lower jaw to enlarge, the chin slopes backward (Fig. 519). Long before puberty it pushes forward until the angle it forms with the lower jaw is not far from a right angle. In adult life the chin projects forward, until finally in old age, with the loss of teeth and the resorption of the alveoli, it projects at almost an acute angle. These successive changes which an individual passes through during a lifetime are strikingly paralleled in the evolutionary emergence of the human race, as shown in Figure 520. The chinless jaw of the gorilla is followed by the almost equally chinless jaw of the Heidelberg man and that, in turn, by the right-angled chin of the *Spy man* from Neanderthal days, to be finally superseded by the projecting chin of modern man, in which there is less standing room for teeth but a greater space within for the attachment of muscles concerned with speech.

VIII. THE LOCOMOTOR SKELETON

1. The Necessity for Animal Locomotion

Attention has already been called in a general way to the necessity for locomotion among animals as contrasted with plants.

The essential difference between plants and animals with reference to locomotion is that green plants by the aid of chlorophyll, which makes them green, are able to imprison the sun's energy by building up into organic foods inorganic compounds that are universally distributed. In consequence they waste no energy in locomotion and have a generous supply of food available for growth and reproduction as well as a surplus for animals. Animals, on the contrary, without the Aladdin's lamp of chlorophyll, must seek their food directly or indirectly, and usually with locomotor effort, wherever plants have made it. Otherwise they perish.

The chemical elements common to all protoplasm, and therefore the food of both animals and plants, are well-nigh universal in distribution in the form of carbon dioxide in the air, water, and various salts and substances in the soil (Fig. 521), while sunlight, the primal source of all energy possessed by organisms of any and every kind, shines alike upon both plants and animals. Since, however, plants alone can utilize the sunlight in transforming these elements into food, and since they can do this in a stationary

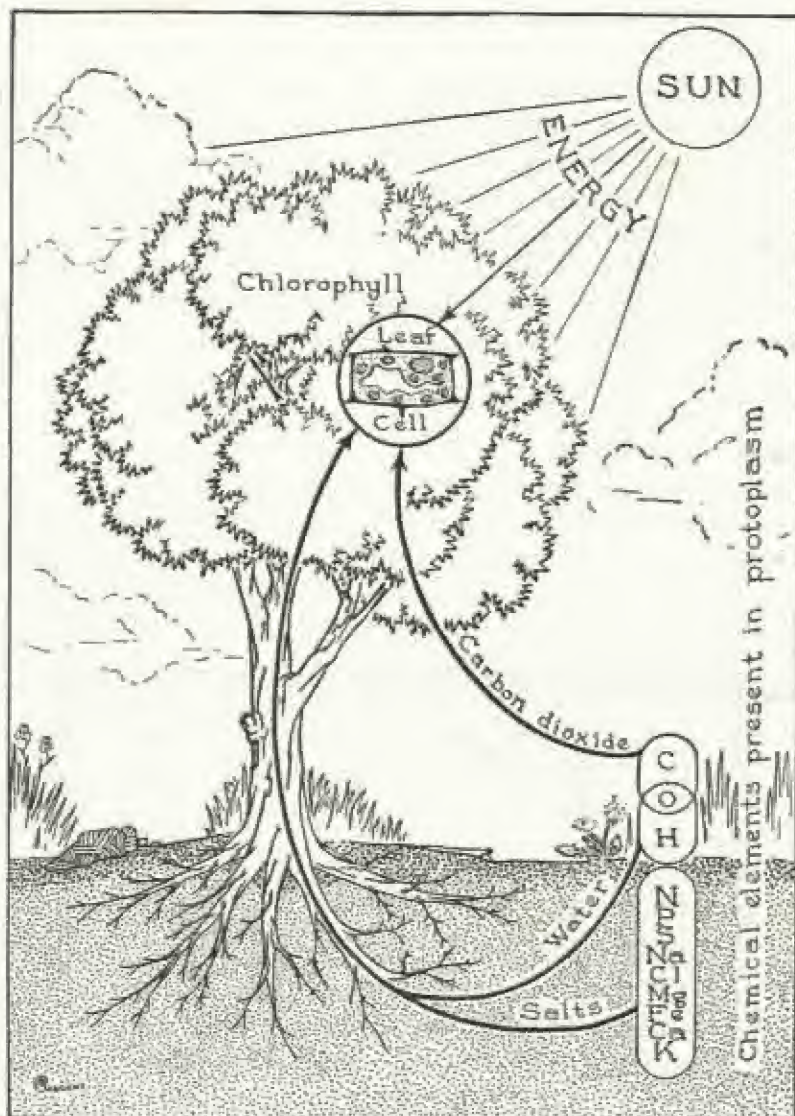


Fig. 521. The "Aladdin's lamp" of chlorophyll.

position, they do not need to move about for their daily bread, while plant-dependent animals do.

2. Evolution of Locomotor Devices

Before skeletal muscles and locomotor levers were arrived at in vertebrates, many other devices for accomplishing motion and locomotion were tried out, more or less successfully, in the animal kingdom.

The inherent contractility of protoplasm is demonstrated even by the modest pseudopods of *Amoeba*. In the microscopic universe of a drop of water other kinds of protozoans also are seen to have speeded up their movements by employing cilia and flagella. Such structures are still retained among higher forms to produce motion even when they are no longer available in locomotion, as for example, cilia bringing food particles into the gullet of a sedentary clam, or removing particles from the respiratory passages of air-breathing animals.

The acrobatic *Hydra*, as described as early as 1744 in the remarkable *Memoires* of Tremblay, pioneer observer and experimenter with Lilliputian life, gaily progresses along the under side of the surface film of water by the method of turning somersaults (Fig. 522). Writhing worms and wiggling vertebrates of one kind or another fill in another chapter in the story of locomotor evolution, but it was when vertebrates emerged from water to land, and levers in the form of legs came upon the scene, that the greatest advance in locomotion was initiated. Once out of water animals could no longer go forward fin-fashion by lateral tailstrokes, for the air is not a sufficiently dense medium to make such strokes effective.

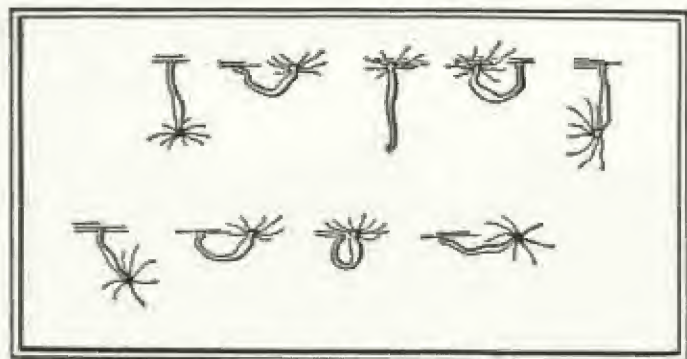


Fig. 522. Acrobatic *Hydra* traveling on a surface film of water. (After Tremblay.)

Considerable time elapsed during the transition from water to land before the lateral legs of primitive land vertebrates assumed a vertical position underneath the body, and sufficient strength and stability were developed to raise the body off the ground. Even then elongated animals, like salamanders and alligators, for example, made little attempt to bear the weight of the body on the legs. Since these appendages extend somewhat laterally, like oars from a boat, they were used principally to push the animal along, with the weight of the body resting on the ground (Fig. 523). After the weight-bearing function finally became established, nature tried

many experiments with locomotor levers all the way from the sprawling plantigrade foot of amphibians, reptiles, and less specialized orders of mammals (Figs. 570 and 573), to that of the wonderfully specialized horse, which stands stilted on the tips of single digits, one at the end of each leg (Fig. 524).



Fig. 523. A salamander showing weak lateral legs which push the body along without lifting it off the ground. (After Morse.)



Fig. 524. The unguligrade foot of a horse.

3. Kinds of Appendages

Vertebrate locomotor appendages, which are fewer and less specialized than those of invertebrates, may be paired or unpaired. The latter sort, confined to water animals, are the more primitive, taking the form of *median fins*, which are either continuous, as in amphioxus, or broken up into separate *dorsal*, *caudal*, and *ventral* fins (Fig. 14), as in fishes.

In addition to median fins fishes normally have two pairs of *paired fins*, namely, *pectoral* and *pelvic*, which are homologous with the locomotor appendages of land vertebrates.

Since paired fins take no part in bearing the weight of the body, supported as it is by the water medium, they are not placed in the same key positions as are the legs of a quadruped, but instead may appear on the sides of the body at widely varying points in different species. With the earliest development of a neck in land animals the pectoral appendages tended to shift backward, but in fishes particularly, the pelvic appendages are apt to move forward from the normal position. In a case as extreme as that of the cod, *Gadus*, the pelvic fins became placed even anterior to the pectoral fins, that is to say, the "hind legs" of a codfish are in front of its "front legs" (Fig. 525).

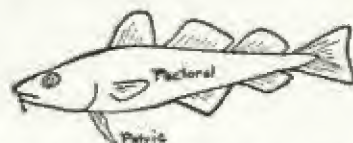


Fig. 525. Outline of a codfish, *Gadus*, the hind legs (pelvic fins) of which are in front of the front legs (pectoral fins).

Both the unpaired and the paired fins of fishes are used primarily either for propulsion or to prevent rotation of the animal on its long axis and to steer it. Propulsion is usually taken care of by the caudal fin as part of the powerful tail. None of the vertebrates has more than two sets of paired appendages, while several have only one, for example, whales and sea cows with only pectorals, and that famous wingless New Zealand bird *Apteryx*, which possesses only the rudiments of a wing skeleton. A few vertebrates, notably snakes, caecilians, and legless lizards, lack appendages of any kind, although some snakes, pythons for example, have rudiments of the pelvic appendages.

4. Origin of the Girdles and Appendages

Concerning the origin of paired fins, the forerunners of all vertebrate appendages, the two most prominent theories have been Gegenbaur's *gill-arch theory*, which now seems to have too little evidence to support it, and Thacher's *fin-fold theory*, which fits in with the known facts of embryology and palaeontology as well as of comparative anatomy. According to the latter theory there was a median unpaired fold extending from the head along the entire length of the dorsal side of the animal, around the tip of the tail, and forward as far as the anus (Fig. 14). In addition, along the ventro-lateral regions of the trunk there was a pair of folds, converging posteriorly, which may or may not have met at the level of the anus and have joined the ventral part of the unpaired fold at that point. From this primitive plan, the set of individual fins, both paired and unpaired, may be derived by the dropping out of some portions and the increased development of others.

The embryonic development of one of the pelvic fins of a dogfish, which more or less parallels the evolution of paired appendages according to the fin-fold theory, may be divided into a series of arbitrary stages that pass continuously from one into the next. These stages are: (1) epidermal ridge; (2) fin fold; (3) mesenchymal invasion; (4) muscle-bud penetration; (5) cartilage formation; (6) concentration; (7) concretion; and (8) union.

First an *epidermal ridge* appears as a narrow, longitudinal elevation, frequently extending over many more segments than will participate in the formation of the fin. In some elasmobranchs such a ventro-lateral ridge develops along the entire length of the trunk (Fig. 526).

In the anterior and posterior portions of the ridge region large *fin folds* of the body wall appear. From these folds, pectoral and pelvic fins, respectively, will develop, while the middle section of the ridge will disappear.

Mesenchymal invasion of the fold is soon followed by *muscle-bud penetration* during which one or two buds grow into the fold from each myotome adjacent to this region.

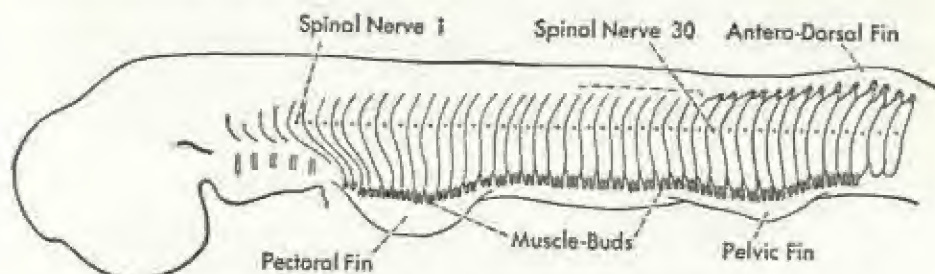


Fig. 526. Embryo of the dogfish *Scyllium*, showing myotomes sending out muscle-buds along entire trunk region. (After Goodrich.)

Between successive muscle buds *cartilage formation*, through the activity of mesenchymal cells, takes place, giving rise to more or less parallel rows of elongate *radial cartilages* (Fig. 527). At approximately the same time, a *concentration*, or crowding of structures, in the base of the fin occurs due to the failure of this basal region to keep pace, in its growth, with the rest of

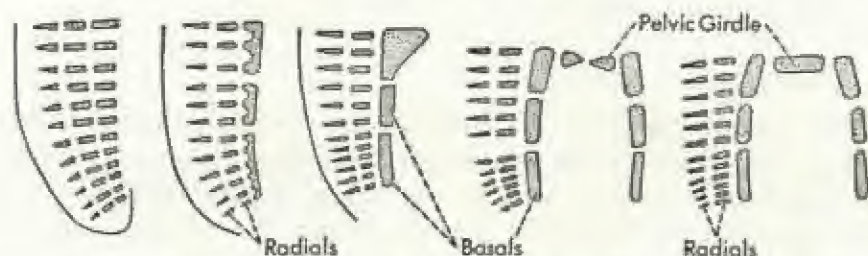


Fig. 527. Diagrams showing limb girdles arising by the concentration, splitting off, and fusion of basal cartilages. (After Hyman and Thatcher.)

the fin and with the body proper. It is believed that in the course of evolution a *conrescence*, or fusion, of the crowded basal portions of the primitive radials gave rise to the large *basal cartilages*. In development these three stages are telescoped together, instead of following one after the other, so that by the time the procartilaginous stage is reached there is a continuous basal mass from which extend out finger-like processes in which the radials will develop (Fig. 528).

Up to this point the development of the median fins parallels rather closely that of the paired fins, as might be expected if all of these appendages are but localized enlargements of one continuous system. The basalia of the

median fins extend into the body to come in contact with the vertebral column with which they articulate permanently. The basalia of the paired fins, in the absence of other hard skeletal parts in the ventral region of the body, undergo further modification. The most anterior basal enlarges and extends into the ventral body wall until it meets the corresponding part of the opposite side with which it fuses. As a result of the union of these two basals a transverse bar, a primitive girdle, is laid down (Fig. 527).

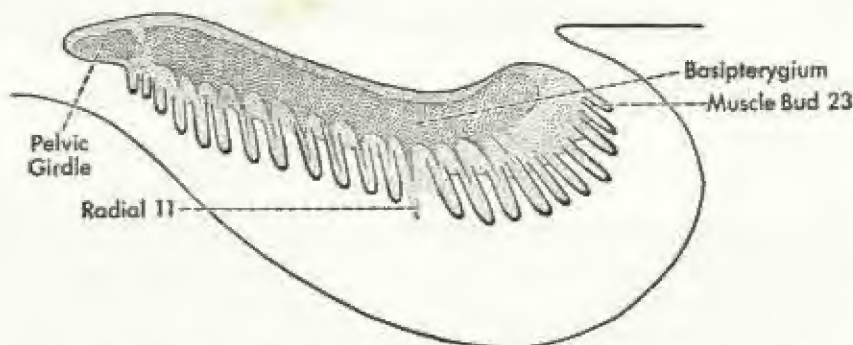


Fig. 528. Pelvic fin of a *Scyllium* embryo slightly older than that shown in Figure 526. Muscle-buds overlying radials are shown in outline except over radial 11. (After Goodrich.)

5. Homology and Adaptation

The paired appendages of vertebrates above the fishes are all built on the same plan, that is, of the same sequence of bones. This consists typically of a tripod of bones known as the *girdle*, which is intermediate between the appendage and the backbone; a large shaftlike bone, called either the *humerus* or *femur*, according to whether it occurs in the anterior or the posterior pair of appendages; two long bones side by side, the *radius* and *ulna*, or the *tibia* and *fibula* respectively; a complex of several small bones, making the *wrist* or *ankle*; a set of five long slender bones, forming the *palm* or the *sole*; and lastly, at the tip of each of the palm or sole bones, two, three, or more small cylindrical bones, placed end to end, known as the *digits* or *phalanges*. For a diagrammatic representation of this sequence of bones in the appendages of a land vertebrate, see Figure 529.

The principal joints or landmarks of the locomotor skeleton in man are indicated in Figure 530.

Each bone of any appendage has its counterpart not only in the appendage on the opposite side, but also in the appendage in front of, or behind it, as the case may be. The similarity from side to side is spoken of as

bilateral homology, while antero-posterior correspondence of parts is called *serial homology*.

Not only may homology between the bones that make up the locomotor appendages of a single individual be established *inter se*, but the leg or arm bones of one vertebrate may be homologized with those of an entirely different species of quite unlike external aspect. For example, each bone in the flipper of a whale or a seal, as well as in the wing of a bird, or even in the foreleg of a horse or a dog, has its homologue in the human arm.

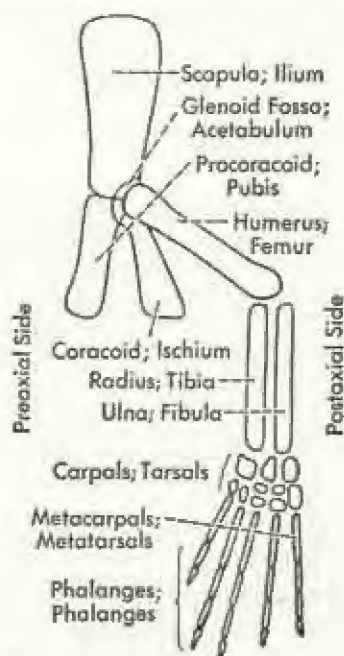


Fig. 529. Diagram showing the homologies of vertebrate appendages. In each label the first-named element is that of the anterior appendage; the second-named, of the posterior appendage.



Fig. 530. The principal landmarks of the locomotor skeleton. (After Hanke.)

Although fundamentally alike, vertebrate appendages exhibit a great diversity, which is associated with the wide range of function that they perform. Climbing trees, burrowing in the ground, swimming in water, jumping, flying, running, standing, striking, lifting, and grasping things, as well as many other kinds of activity, call for particular modifications of the type.

6. The Comparative Anatomy of Girdles

(a) **Girdles in General.**—Excepting in elasmobranchs, the *girdles*, or intermediary bones between the body and the limbs, are originally made up of three bones on either side (Fig. 529), which meet in the form of a tripod at a common point where the free limb articulates. The triple character of the girdles is best seen in reptiles, especially in some extinct fossil forms, rather than in mammals where drastic modifications have taken place.

In the *pectoral*, or *anterior girdle*, there is usually no articular connection with the main axial skeleton. The girdle is laced to the anterior part of the thoracic basket by means of ligaments and muscles. It may articulate with the sternum, as for instance in man, but never with the backbone except in rays and in certain pterosaurs.

The *pelvic*, or *posterior girdle*, on the contrary, except in fishes, always articulates with the backbone, through the medium of the "sacral ribs" (Fig. 443). This difference in attachment gives a greater range of motion to the pectoral appendages and a firmer support to the pelvic appendages, which in many cases, particularly in bipeds, bear the greater weight of the body.

The three girdle bones of each pectoral appendage occupy positions of serial homology with respect to the girdle bones of the pelvic appendages. Thus, one bone, respectively the *scapula* or the *ilium*, extends dorsally; another, the *procoracoid* or the *pubis*, is placed antero-ventrally; and a third, the *coracoid* or the *ischium*, postero-ventrally.

The articular cup for the front leg at the junction of the three pectoral girdle bones is called the *glenoid cavity*, while the corresponding articular fossa on the pelvic girdle for the reception of the hind leg by reason of its hollow shape has been named the *acetabulum*, or "vinegar cup."

Although at first modeled in cartilage, all of these girdle parts afterwards become replaced by bone. They, therefore, belong to the category of replacing bones, similar to those of the inner skull. There are, however, certain additional bones of investing character in the pectoral girdle of fishes, as well as in other vertebrates including man, which put in their appearance without preliminary blue prints in cartilage. The principal one of these is the *clavicle*, which is substituted for, or takes over the work of, the procoracoid. The fact that it is not a transformed procoracoid but, instead, a new bone of entirely different origin, is demonstrated by the pectoral girdle of the European toad *Bombinator* (Fig. 531), in which the procoracoid and the clavicle are both found present at the same time.

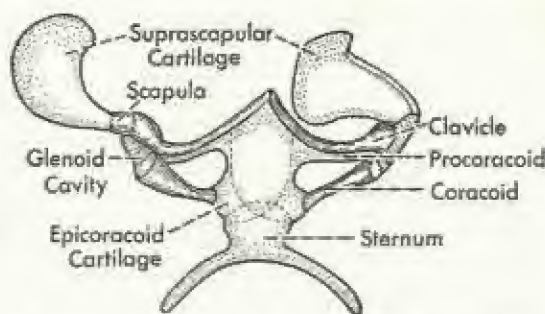


Fig. 531. The pectoral girdle and sternum of a European toad, *Bombinator*, showing the clavicle taking the place of the procoracoid. The left suprascapular cartilage and scapula (in the right-hand portion of the figure) are in natural position; the right ones have been swung ventrally. (After Wiedersheim.)

(b) **Pelvic Girdle.**—Unlike the pectoral girdle the pelvic girdle has nothing corresponding to the thoracic basket with which to become involved. It is concerned solely with its hook-up to the vertebral column. Like its pectoral homologue it consists typically of three parts, a dorsal element, the *ilium*, and two ventral elements, of which the *pubis* is anterior and the *ischium* posterior, forming tripods on either side for the articulation of the hind legs (Fig. 529). All three pairs of pelvic girdle bones are replacing in

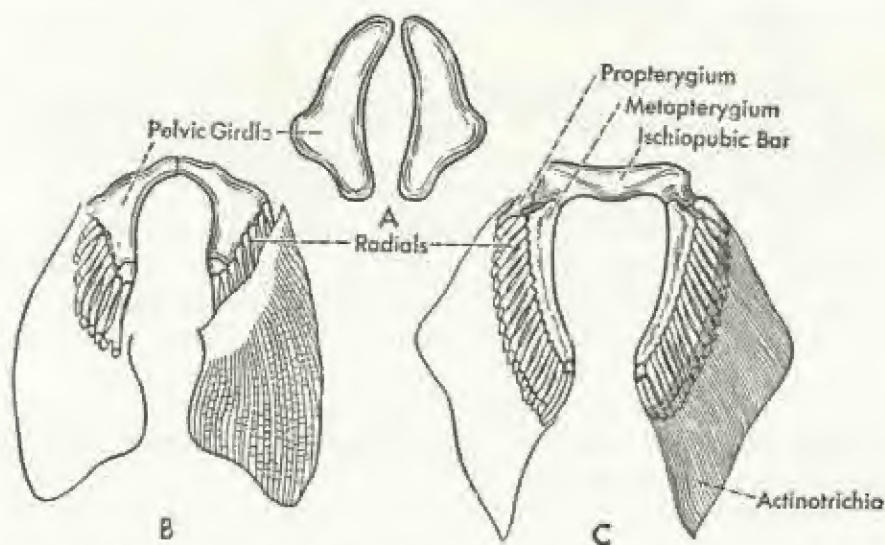


Fig. 532. Evolution of the pelvic girdle in fishes. A, a fossil elasmobranch, *Pleuracanthus*; B, a chondrosteian, *Acipenser*; C, a modern dogfish, *Squalus*. (A and B, after Goodrich.)

character. Their typical relation to each other and to the backbone undergoes some striking modifications in the vertebrate series.

The pelvic girdle in fishes, when present, is very simple, as would be expected, serving merely as a support for the pelvic fins without making connection with the axial skeleton. In elasmobranchs and cartilaginous ganoids it is a flat central bar of cartilage (Fig. 532c), the origin of which is suggested by *Pleuracanthus*, a fossil elasmobranch (Fig. 532A), as well as by *Acipenser*, a chondrosteian (Fig. 532B); in which two enlarged cartilaginous plates approach each other on the ventral side of the body without

uniting. In the Holocephali the two parts do not fuse but are connected by a ligament, and each bears an *iliac process* extending dorsally from the region of fin attachment.

The Dipnoi, as represented by *Protopterus* (Fig. 533), have a median ventral cartilaginous *ischio-pubic plate* of bilateral origin serving as the pelvic girdle, with six processes extending from it.

Stegocephalians (Fig. 534), pioneers among walking tetrapods, possessed a broad ischio-pubic plate similar to that of the dipnoans, but composed of two pairs of bones, the large *ischia* that replaced

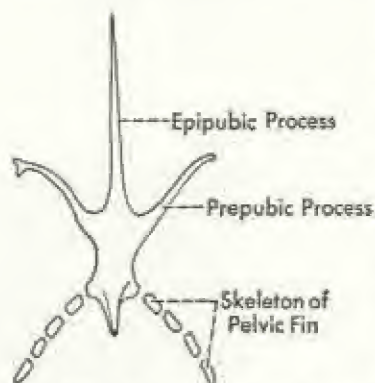


Fig. 533. Ventral view of the pelvic girdle of *Protopterus*. (After Wiedersheim.)

the cartilage in the posterior region of the plate and smaller *pubes* in the anterior part. In each pubis was a small *pubic foramen* through which the obturator nerve passed. Two separate *iliac bones*, which replaced the iliac processes, extended dorsally to reach the vertebral column.

Urodeles, in common with most modern amphibians, have bony *ilia* and *ischia* but cartilaginous *pubes*. The ilia reach the single sacral vertebra (except in *Proteus* and *Amphiuma* which have degenerate hind legs), joining it by means of a pair of small intermediate parts known as *sacral ribs* (Fig. 535). *Pubic foramina* are also present.

In some urodeles, for example *Cryptobranchus*, there appears, in the midventral *linea alba*, an independent Y-shaped *ypsiloid cartilage* that connects secondarily with the pelvic girdle.

Although considerable modification of the pelvic girdle takes place in most anurans due to their hopping and jumping methods of locomotion, the African toad, *Xenopus* (Fig. 536), shows a generalized pelvic girdle with three pairs of contributing bones all typically ossified from cartilaginous

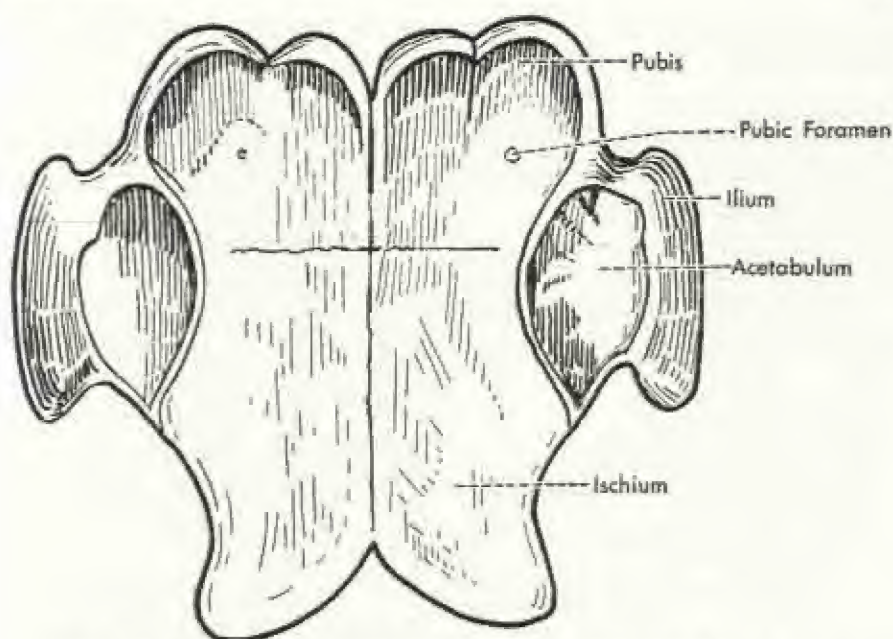


Fig. 534. Ventral view of the pelvic girdle of a stegocephalian, *Cacops*. (After Williston.)

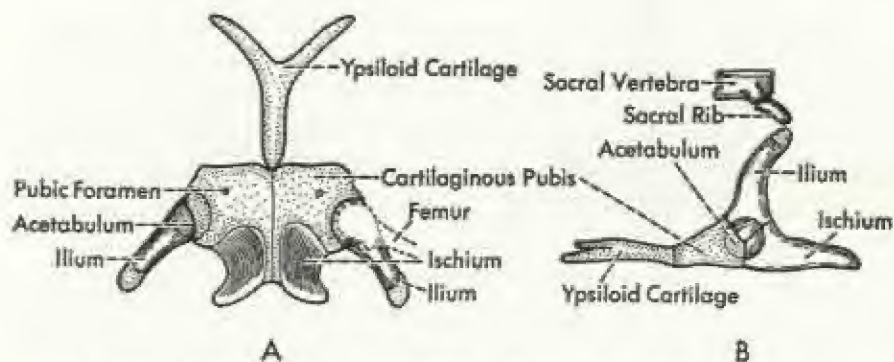


Fig. 535. Pelvic girdle of a salamander, *Salamandra*, showing sacral rib. A, ventral view; B, left-lateral view. The cartilage is dotted. (After Wiedersheim.)

forerunners, and, in addition, the ypsiloid cartilage, which in this case is not forked but spatulate in shape.

In the frog *Rana*, however, the three pairs of pelvic elements form a U-shaped structure that connects the jumping legs with the single sacral vertebra (Fig. 438). *Ilia* and *ischia* are bony, while the *pubes* are composed of calcified cartilage. The legs are articulated on either side of a round

disc, which is made up of components from all three pelvic elements so welded together that the pubic foramen is obliterated entirely. From this disc springs upward a pair of swordlike extensions, the ilia, that reach the vertebral column which teeters up and down suspended between their tips, thus absorbing in part the shocks that would otherwise reach the brain when the jumping frog lands.

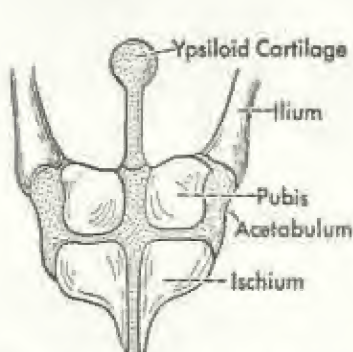


Fig. 536. Pelvic girdle of African toad, *Xenopus*. (After Wiedersheim.)

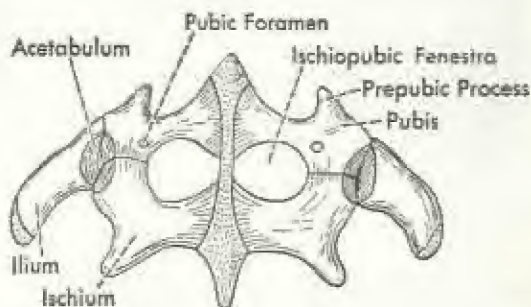


Fig. 537. Ventral view of pelvic girdle of *Sphenodon*, showing ischiopubic fenestra or foramen. (After Wiedersheim.)

In reptiles all of the pelvic bones are well developed and distinct. In many there is a symphysis, or union, of both pubic and ischiac bones along the midventral line although frequently a large open space, the *ischio-pubic fenestra*, develops on either side between the pubis and ischium resulting usually in a complete separation of *pubic* and *ischiac symphyses* (Fig. 537). In crocodiles only an ischiac symphysis occurs, the pubic bones remaining slightly separated (Fig. 538).

A pubic foramen persists in *Sphenodon*, the plesiosaurs, and lizards; but in turtles and crocodiles it combines with the ischio-pubic fenestra into a common opening separated from its mate on either side by a median ligament, and is then termed the *obturator foramen* (*foramen obturatum*).

In crocodiles the pubis does not participate in the formation of the articular cup, or *acetabulum*, for the attachment of the hind leg. This cup is perforated by an *acetabular foramen* in crocodiles, birds, and monotremes, but not in mammals generally. Ichthyosaurs, which used their tails in swimming, as well as cetaceans and sirenians that have no use for hind legs, are characterized by a greatly reduced pelvis since locomotion is not dependent upon it.

Among the legless snakes the pythons alone retain a trace of the pelvic

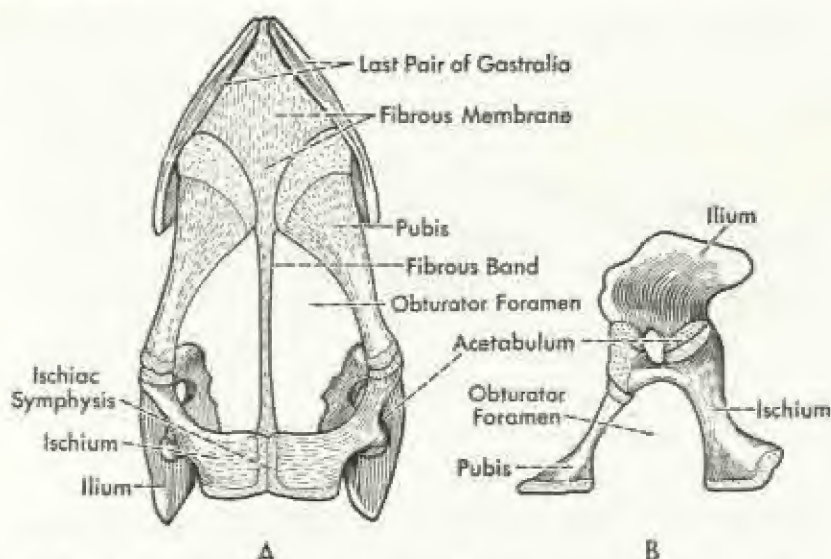


Fig. 538. Pelvic girdle of a young *Alligator*. A, ventral view; B, left-lateral view. (After Wiedersheim.)

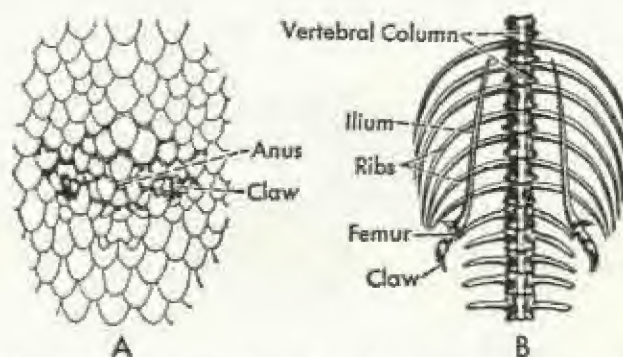


Fig. 539. Vestigial hind limbs of a python. A, ventral view of surface of body, showing claws; B, skeleton, showing rudimentary appendages. (From Neal and Rand, *Comparative Anatomy*, copyright 1936, by permission of P. Blakiston's Son and Company, publishers. After Romanes.)

girdle, reminiscent of the remote past when the ancestors of snakes walked (Fig. 539).

Dinosaurs among the reptiles of the past gave prophecy of the modifications which characterize the pelvic girdles of birds. For example, the girdle of the fossil reptile *Stegosaurus* (Fig. 540) shows a spreading fan-shaped ilium, a long ischium extending posteriorly without a symphysis, and a backward-projecting pubis on either side that runs parallel to the ischium instead

of meeting anteriorly and ventrally in a pubic symphysis. The place of a typical pubis in some instances is partly filled by an anterior prepubic process.

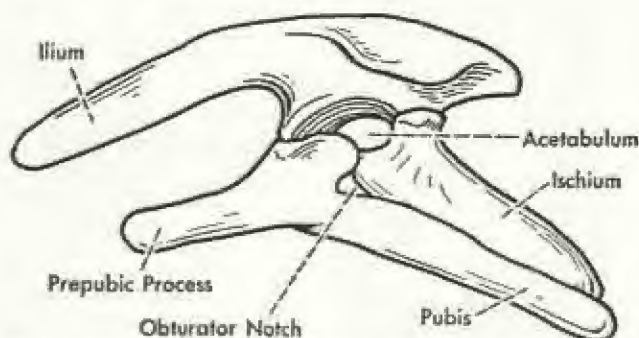


Fig. 540. Pelvic girdle of *Stegosaurus*. Left-lateral view. (After Marsh.)

Modern birds exemplify all of these features, with the ilium enormously expanded and brought in contact with many vertebrae. The prepubic processes are reduced or absent (Fig. 541). In the embryo of the bird the pubic bones at first extend transversely, approaching each other as if a

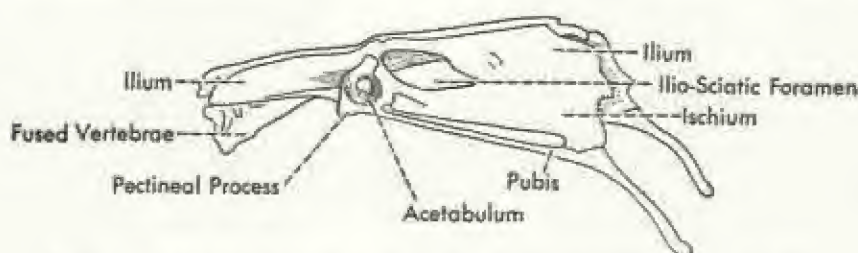


Fig. 541. Left-lateral view of pelvic girdle and sacrum of a duck, *Anas*, showing reduced prepubic (pectineal) process. (After Reynolds.)

symphysis or junction were to follow (Fig. 542), but by the time the adult condition is reached, they have spread apart and come to project backward, as in *Stegosaurus*, thus allowing for an unobstructed passage of large eggs with breakable calcareous shells. Long before the expeditions to Mongolia that unearthed the famous dinosaur eggs now reposing in the American Museum of Natural History in New York City, the spreading pubic bones of these fossil reptilian giants made it possible to guess with reasonable certainty that in their day and generation they laid sizable eggs with calcareous shells.

The primitive character of the earliest known bird, *Archaeopteryx*, is clearly shown by its small pelvic girdle bones with distinct sutures between them and by the presence of an unbirdlike pubic symphysis (Fig. 543), as well as by the fact that the ilia connect with only six vertebrae, instead of the larger number characteristic of modern birds. The only other bird with a symphysis pubis is the African ostrich, *Struthio*, while an ischiac symphysis occurs only in the South American ostrich, *Rhea*, in which the symphysis lies dorsal to the digestive tract.

In mammals generally the three embryonic bones on either side of the pelvic girdle fuse together to form the single *innominate bone* (Fig. 544). Where the innominate bones of the two sides meet ventrally, the monotremes, marsupials, many rodents, insectivores, ungulates, and carnivores have a *symphysis ischiaticum*, as well as a *symphysis pubis*, but in primates, while the pubic bones unite in a symphysis, the ischia separate, forming two posterior skeletal projections that support the sitting animal. It would

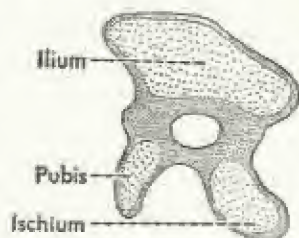


Fig. 542. Left-side view of the pelvic girdle of an embryo bird showing the natural position of the pubis before its backward migration. (After Mehnert.)

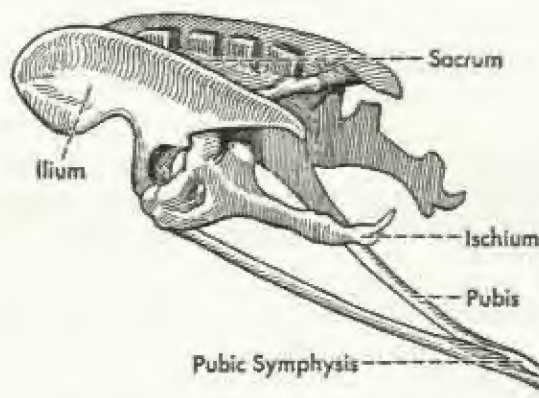


Fig. 543. Oblique view, from the left and posterior, of the pelvic girdle and sacrum of *Archaeopteryx*, restored. (After Heilmann.)

be extremely awkward for a cow, even if so minded, to "sit down" upon the single sharp ridge formed by the fusion of the two ischia. The large *obturator foramen*, formed by the union of pubic and ischio-pubic openings, is closed by a strong connective-tissue membrane except for a small passage-way, at its anterior end, through which the obturator nerve and blood vessels pass.

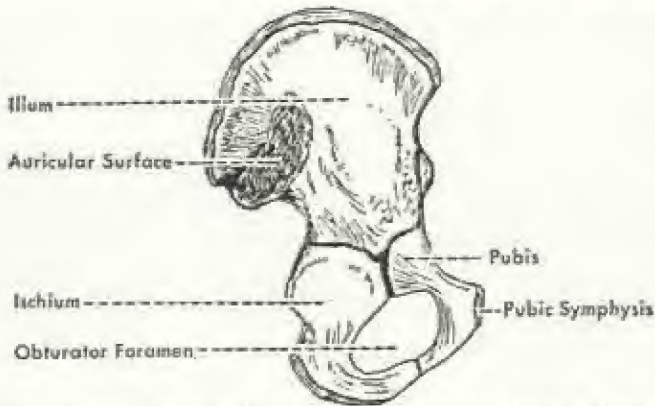


Fig. 544. Inner surface of the innominate bone of a child of eight years. (After Morris.)

TABLE IX

	a to b	c to d
♂	12.7 cm	11.2 cm
♀	14.5 cm	12.7 cm

The large fan-shaped ilium of man articulates, at an ear-shaped *auricular surface*, with the sacrum formed from five sacral vertebrae and their

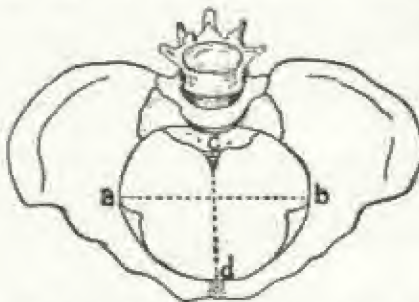


Fig. 545. Outline of the female pelvis. *a-b* and *c-d*, two diameters of the inferior pelvic aperture. (After Cunningham.)

ribs. The two innominate bones, together with the sacrum and coccyx, form the *pelvis*, a somewhat funnel-shaped basin with a large anterior opening and a smaller posterior one. Through this bony halo must pass every mammal that is normally born into the world. In the female, the anterior parts of the ilia have a greater spread than in the male, giving as a result not only a shallower pelvic basin but broader hips. There are also distinguishable sexual differences in the

posterior opening, which for obvious reasons is relatively larger in the female than in the male. Rauber gives the average comparative dimensions in man shown in Table IX, in which the letters refer to Figure 545.

The human pelvic girdle is for many reasons perhaps the most character-

istic and distinctive part of the human skeleton, recording as it does drastic adaptations as the result of upright posture. Its triple composition is apparent embryologically for it is not until about the time of puberty that the three elements on either side become completely fused into the innominate bones, which together with the sacrum and coccyx of the vertebral column make up the pelvis. A firm, bony bowl immovably attached to the vertebral axis is thus formed in a position that not only provides attachment for the legs but also supports the viscera.

The spread of the iliac portion of the pelvis is greater among higher races than among primitive peoples, and in quadrupeds, where the weight of the viscera does not bear so directly on the pelvis, the iliac bones are narrower and do not flare so far apart.

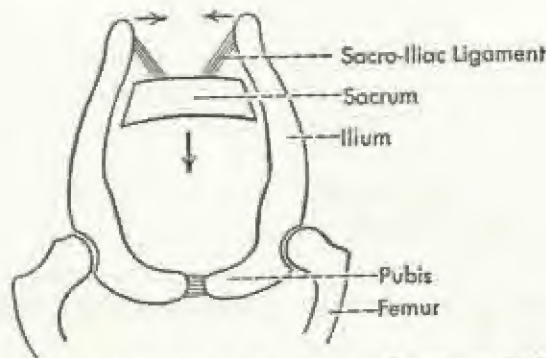


Fig. 546. Diagram showing the sacrum as a keystone which, although upside down, nevertheless functions as such by reason of the action of the sacro-iliac ligaments; since the greater the weight from above, the more the iliac bones tend to pinch together, thus holding the sacrum in place. (After Meyer.)

The curving heads of the two femurs form, with the innominate bones, part of an arch which is completed above by the sacrum as a keystone (Fig. 437), which resembles a wedge upside down. On this arch the weight of the entire body is supported. The faults of this mechanical curiosity, as pointed out by Meyer, are corrected by means of *sacro-iliac ligaments* that extend from the sacrum to the upper edge of the ilium (Fig. 546). When the weight of the body presses down upon the sacrum it pulls upon these ligaments with the result that the iliac bones pinch together like a vise, thus holding the upside-down keystone firmly in its place. The greater the weight the more firmly the sacrum is held.

Monotremes and marsupials have an additional pair of pelvic replacing bones, called *marsupial bones*, the origin of which is unknown. It has been

suggested that they may be transformed *gastralia*, or abdominal ribs. The fact that, unlike the abdominal ribs of reptiles, they are replacing instead of investing bones is not favorable to this supposition. Furthermore, no trace

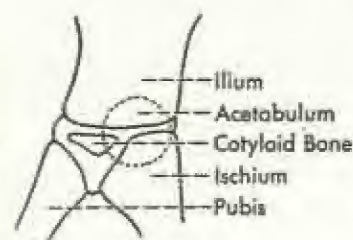


Fig. 547. Pelvic girdle of a civet cat, *Viverra*, showing the acetabular, or cotyloid, bone. (After Wiedersheim.)

of them is found in placental mammals. Although they are doubtless useful in supporting the pouch of the female marsupial, they are not primarily utilized for that purpose, since they are equally well developed in both sexes. Whatever part they may play for their possessors, they are definitely of service to the comparative anatomist in enabling him to distinguish the skeleton of a marsupial from that of a placental mammal.

The *acetabular*, or *cotyloid*, bone, an additional small bony element which enters into the formation of the acetabulum in mammals (with the exception of monotremes, rodents, and bats), ossifies later than the other component parts of the pelvic girdle (Fig. 547).

(c) **Pectoral Girdle.**—The pectoral girdle has evolved further from the primitive set-up and is somewhat more complicated than the pelvic girdle, not only because of its secondary relations with the sternum and comparative freedom from the backbone, but also because investing as well as replacing bones take part in its formation.

It has its rise in the lower aquatic vertebrates, just posterior to the region weakened by the perforations of the gill slits. Hence the need for supplementary investing bones at this point was much greater than in the region of the pelvic girdle.

The ventral anchorage to the sternum of the *clavicles*, which in man are involved in providing an adequate support for the arms, is such that interference with the free respiratory movements of the ribs is largely removed.

Since there are no girdles of any kind either in amphioxus or the cyclostomes, the point of evolutionary departure for the pectoral girdle, as for so many other anatomical features, is found in the clasmobranch fishes, where a horseshoe-shaped bar of cartilage with its points extending upwards dorsally hooks under the "throat" just posterior to the gill arches. On either side of this inverted arch the paired pectoral fins articulate about midway from the tip to the ventral point of junction. The part above the attachment of the fin on either side (Fig. 548) is the *scapular process*, while that below, which joins the two halves of the arch ventrally, is the *coracoid bar*. In skates and rays, but not in dogfishes and sharks, the dorsal end of the

scapular region may articulate with the vertebral column, thereby establishing connection with the axial skeleton, an unusual condition among vertebrates.

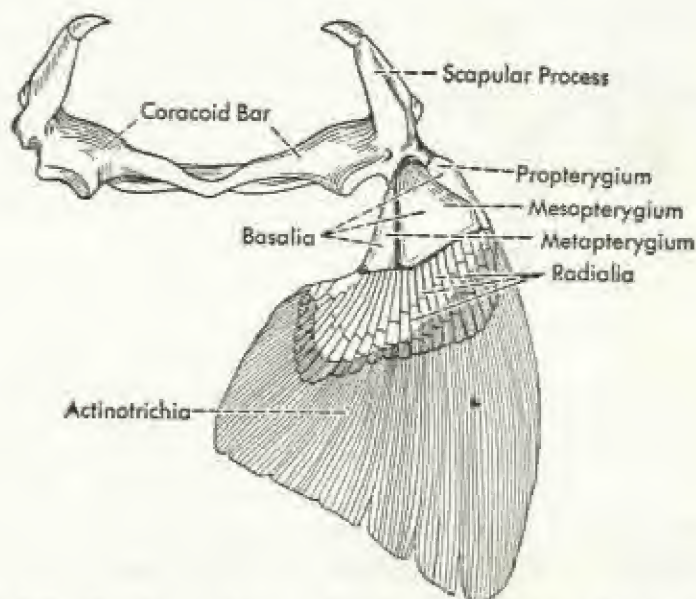


Fig. 548. Dorsal view of pectoral girdle and right fin of *Squalus acanthias*, the spiny dogfish.

The pectoral girdle of ganoids, dipnoans, and teleosts begins with the formation of a pair of *coracoscapular cartilages*, which later become overlaid by investing bones. Primarily there are four of these investing bones in a more or less vertical row on each side of the body, namely, a ventral *clavicle*, then a large *cleithrum*, near the base of the fin, dorsal to which is a *supracleithrum* followed by a *posttemporal* which usually articulates with the posterior part of the skull. With the disappearance of clavicles in holosteans and teleosts (Fig. 491), the cleithra tend to enlarge to meet ventrally. In teleosts, *coracoid* and *scapula* ossify from cartilage as distinct bones, although outside investing bones make up the bulk of the girdle.

The fossil stegocephalians (Fig. 549) unfortunately have only the bony parts of the pectoral girdles left to tell the tale, but these include paired *clavicles* and *cleithra* in addition to a median unpaired *interclavicle* between the ventral ends of the clavicles. The replacing girdle consists of a single pair of *coracoscapular* bones. The anterior appendage articulates on either side in a hollow, the *glenoid cavity*, instead of on a prominence as in elasmobranchs.

The highly specialized urodeles also have a single pair of *coracoscapular* bones although most of the girdle is cartilaginous, including a dorsal *supra-scapula* and a ventral fanlike part of the *coracoid* which overlaps its fellow of the other side (Figs. 460 and 461). Extending forward from the middle of the coracoscapular region is a cartilaginous *procoracoid process* of doubtful homology. In some cases, for example, *Necturus*, the ossification does not extend into the coracoid, being limited to the ventral part of the scapula. Urodeles are without investing girdle bones.

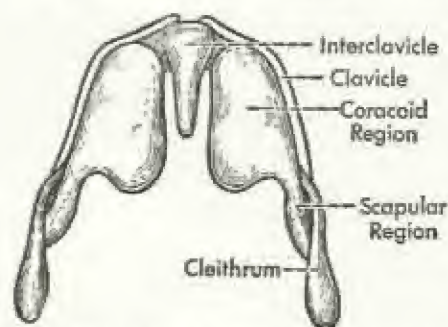


Fig. 549. Dorsal view of the pectoral girdle of a stegocephalian, *Cacops*. (After Williston.)

Among the anurans the median margins of the coracoid and procoracoid cartilages coalesce on each side into an *epicoracoidal cartilage* (Fig. 462). In toads the epicoracoids may overlap or slip past each other after the manner of the coracoids in urodeles, but in frogs they abut on each other or fuse into a common epicoracoidal plate. The procoracoid becomes strengthened externally by an overlying investing bone, the *clavicle*, which eventually takes its place. Both the cartilaginous coracoid and the scapula are replaced by bone, and even the supra-scapula in part, so that there finally result in the pectoral girdle of the frog the following paired bones: clavicles, coracoids, scapulas, and supra-scapulas, together with the cartilaginous epicoracoidal plate, of which parts only the clavicles are investing in character. The ventro-median ends of the clavicles and coracoids are embedded in the epicoracoidal plate, which also fuses with the sternal elements to form a continuous ventral structure.

The primitive reptiles, or cotylosaurs, in contrast with the primitive amphibians, had at least two bones, *scapula* and *coracoid*, in each half-girdle while in some cases a ventral *procoracoid* also ossified in front of the coracoid (Fig. 550). In all cotylosaurs there was a mid-ventral *interclavicle*, a pair of *clavicles*, and usually a small pair of *cleithra*, all of which are investing bones reminiscent of the condition in stegocephalians. The therapsid reptiles, probably ancestral to the mammals, had all three pairs of replacing bones as well as clavicles and an interclavicle but usually lacked cleithra.

In general the pectoral girdle of modern reptiles is more bony than that of amphibians, consisting of replacing *scapulas* and *coracoids* together with

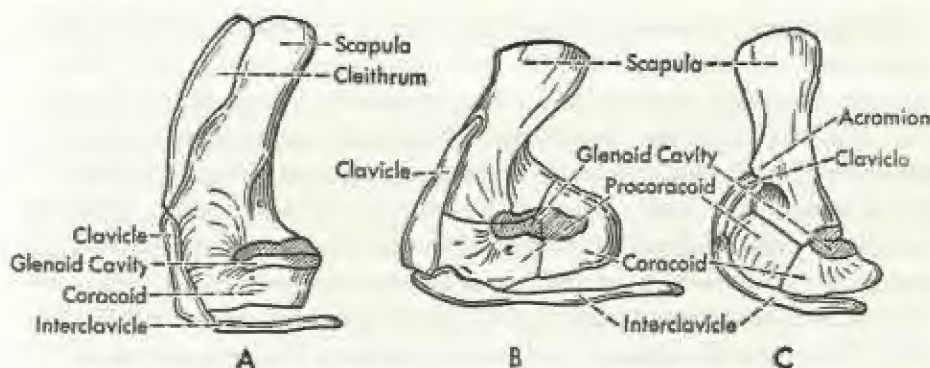


Fig. 550. Left-lateral views of the pectoral girdles of three primitive reptiles. A, a cotylosaur, *Diadectes*; B, a cotylosaur, *Labidosaurus*; C, a therapsid, *Dicynodon*. (After Romer.)

investing *interclavicle* and *clavicles* but never cleithra or procoracoids. The pectoral girdle of turtles consists on either side of a tripod of rodlike bones which lacks the clavicle. The dorsally extending part of the tripod is the *scapula*, and the posterior ventral element, the *coracoid*, but the anterior ventral element, which was formerly taken to be the investing clavicle, is now known to be an outgrowth of the replacing scapula and is termed the *acromion*. It is homologous to the *acromion process* of the mammalian scapula (Fig. 551) with which the clavicle articulates. The *interclavicle* and the *clavicles* are now known to participate in the formation of the *plastron*, the ventral part of the turtle's shell.

The pectoral girdle of turtles is peculiar in another way. The whole structure, as well as the pelvic girdle, is *inside the ribs* which form part of the shell, an arrangement not found among other vertebrates. In the embryos the girdles are still outside the ribs as usual, but with the modification of the ribs into costal plates that flatten out and unite edge to edge to contribute to the carapace, or dorsal part of the shell, the two girdles sink in and are covered over by the expanding ribs.

In crocodiles the clavicle, although appearing in the embryo, does not persist in the adult. The *interclavicle* is a simple rod in crocodiles (Fig. 464) but T-shaped in lizards (Fig. 463). The *coracoid* and *scapula* of lizards are frequently fenestrated, that is, broken up by window-like parts. Pectoral girdles are missing in snakes and much reduced in the legless lizards.



Fig. 551. The left shoulder blade (scapula) of man, as seen from behind. A, acromion process; C, coracoid process; sp, spine; sc, infra-spinous fossa.

Birds, whose extremely flexible necks tend to push back the anterior girdle bones towards the compact centralized region of the body, have a completely ossified pectoral girdle. The *scapula* becomes reduced to a narrow swordlike bone that lies close to the ribs along the dorsal surface of the thoracic basket; the *coracoid* is enlarged into a stout strutlike bone that braces against the upper edge of the sternum on either side; while the *clavicles*, by the medium of an *interclavicular element* joint into a "wish-bone," or *furcula*, which in most cases also anchors onto the sternum, thus making a firm skeletal foundation for the attachment of the wings (Fig. 459). The *glenoid cavity*, or the points on either side between which the body is suspended by the wings, is partly on the scapula and partly on the coracoid, thus insuring adequate articulation.

Ratites, or running birds, show adaptive differences, as compared with carinates, or flying birds, for in these forms both coracoid and scapula are reduced in size and ankylosed together, and the abbreviated clavicles fail to meet in a furcula. In *Pachyornis*, an extinct "moa," the shoulder girdle is entirely absent, and in the living wingless *Apteryx* it is extremely rudimentary.

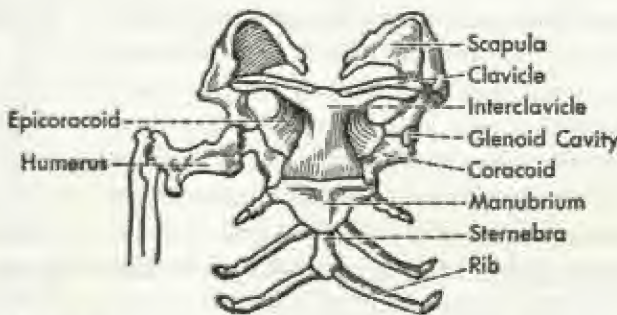


Fig. 552. Ventral view of pectoral girdle and anterior portion of sternum of *Ornithorhynchus*.

There are two types of pectoral girdles in mammals, as exemplified in primitive monotremes and in higher mammals. Monotremes retain the *coracoids* and have a lizard-like investing *interclavicle* intimately connected with the pectoral girdle, while the *scapula* is also quite unmammalian in appearance (Fig. 552). Other mammals lack the coracoid except in the form of the *coracoid process*, which may remain for some time as a separate skeletal element before its final fusion with the scapula. Since the scapulas are the sole bearers of the anterior appendages they become broadened usually into thin flat triangular bones, each characterized by a keel-like

ridge, the *spina scapulae*, for the generous attachment of muscles (Fig. 551).

In mammals such as bats and primates, in which there is great power in the anterior appendages, the clavicles are strong and well developed, connecting the scapulas with the sternum. Diggers, climbers, and flyers belong to the collar-bone fraternity, while the ungulates, adapted for running, and the pinnipedes, sirenians, and cetaceans, aquatic mammals with appendages reduced to paddles, are either without a clavicle or have it much reduced. The clavicles of cats are merely degenerate splintlike floating bones, unattached at either end, so that the free bladelike scapulas may be seen slipping up and down past each other under the loose skin when these animals walk, making great freedom of motion possible for the quick stroke of the carnivorous paw.

7. The Free Appendages

(a) **Unpaired Fins.**—The locomotor appendages of vertebrates may be separated into *single median* and *paired lateral* appendages. The former type reaches its highest manifestation in the unpaired fins of fishes.

The forerunner of the median appendages is seen in amphioxus, where a continuous fin, or integumental fold, supported by connective tissue (Figs. 13 and 14), extends from the antero-dorsal region around the end of the tail, and ventrally to the right of the anus as far forward as the atrial pore. A similar continuous median fin is characteristic of most fishes in early embryonic stages. As development proceeds, portions of this continuous fin are absorbed, leaving isolated parts which form the various *dorsal*, *caudal*, *anal*, and *ventral* fins (Fig. 525). In general these median fins serve, like the centerboard of a sailboat, to maintain an even keel in water. The caudal fin also increases the effectiveness of the lateral stroke of the tail in sculling locomotion.

The paired horizontal fins of skates and rays are expanded, enabling these bottom-dwelling animals to move up and down as well as to swim forward.

The most primitive type of tail fin, found in amphioxus, cyclostomes, and amphibians, is *protocercal* (Fig. 553A), in which the vertebral column remains unbent and the inconspicuous flanges of the caudal fin are practically equal, dorsally and ventrally. In elasmobranchs and some ganoids the end of the skeletal axis curves upward (Fig. 553B), so that the flange of the caudal fin ventral to the vertebral column becomes considerably larger than the dorsal portion. This condition is termed *heterocercal*. The great majority of fishes, however, have a *homocercal* arrangement (Fig. 553C

and *n*), that is, the upturned end of the skeletal axis becomes reduced while the dorsal flange again equals the ventral part. The *diphycercal* tail of living dipnoans is symmetrical externally while the skeletal axis is shortened so much that the upturned part, present in ancestors of these fishes, has been obliterated (Fig. 553E). In long-bodied fishes like squirming eels, the unnecessary tail fin becomes quite degenerate.

Frequently the caudal fin becomes deeply incised, as in the mackerel, *Scomber* (Fig. 553D), or more or less rounded, as in the "mummichug," *Fundulus* (Fig. 553C).

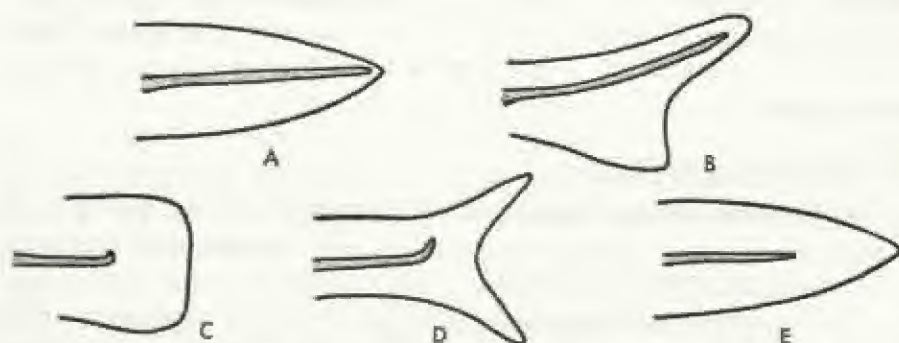


Fig. 553. Different types of tails in fishes. A, protocercal; B, heterocercal; C, D, homocercal; E, diphycercal.

Since all fins must have flexibility, this end is best accomplished by each fin acting as a whole, without the levers and joints that characterize the locomotor appendages of land vertebrates. To bring this about they are braced in position by skeletal elements which lie between the two walls of the fin fold. The most proximal of these supporting elements (*basalia*) connect with the girdle or, in the case of median fins, with the neural spines of the underlying vertebrae secondarily. The more distal elements (*radialia*), which may be either cartilage or bone, splice on to the basalia, thus extending the area of the fin. Radialia of bone may be regarded as derivatives of the bony scales of fishes. Frequently isolated basalia, usually situated directly in front of the fin proper, develop into defensive spines that are augmented by basal poison sacs.

In addition there is present in many fishes still a third kind of fin rays (*actinotrichia*), which are horny in texture, dermal in origin, and double in structure (Fig. 548), one half being derived from either side of the fold of skin constituting the fin. Actinotrichia may entirely replace the radialia, although in most fishes both radialia and basalia appear. The very primitive fin rays of amphioxus are gelatinous in character.

Amphibian larvae, as well as adult perennibranchs, have a caudal fin that may extend some distance anteriorly, but which differs from the caudal fin of fishes in being without skeletal support. Dorsal fins occur in cetaceans (Fig. 75) as they did in ichthyosaurs. Sirenians as well as cetaceans develop caudal appendages, usually spoken of as *flukes*, which are horizontal rather than vertical in arrangement (Figs. 72 and 73). Like the caudal fins of amphibians, all these special appendages of mammals are unsupported by fin rays of any kind.

(b) **Lateral Appendages in General.**—Typically there are two pairs of lateral appendages in all vertebrates. They serve a great variety of uses aside from the primary function of locomotion.

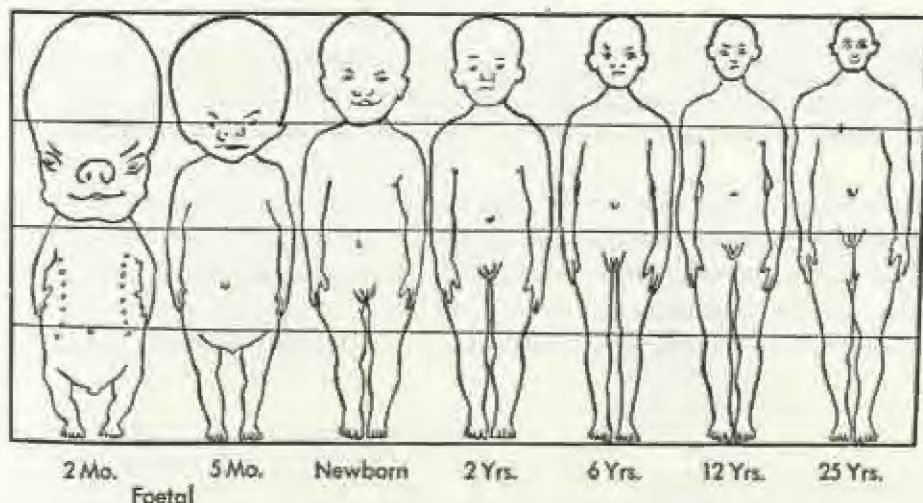


Fig. 554. Figures illustrating changes in body proportions during prenatal and postnatal growth. (After Stratz.)

Of vertebrates without paired appendages, the cyclostomes represent a primitive condition. Other legless vertebrates, such as caecilians, snakes, and certain lizards when adult, may be said to be reduced secondarily to this state, for some of them have appendages, at least in their early stages. Legs have been found, for instance, in the embryo of the apodous amphibian, *Gymnophiona*, by P. and F. Sarasin.

A few vertebrates have only anterior appendages. The list includes the chondrostean *Calamoichthys*; representatives of the teleost order of Apodes; the caudate *Siren*; the lizard *Chirotis*; the orders of Sirenia and Cetacea (although Kükenthal found hind legs in the embryo of one species of whales); and some other forms.

A smaller list of vertebrates, having only posterior appendages, include pythons and boa-constrictors with rudimentary hind legs embedded in the skin; the lizards *Pygopus* and *Pseudopus*, and possibly some other forms. The Australian burrowing "kiwi," *Apteryx*, although regarded as wingless, shows vestigial anterior appendages.

The relative length of arms and legs in man as well as head and trunk varies with age (Fig. 554). Eventually the legs, which at first are shorter than the arms, come to be longer, so that it is not easy for man to assume the

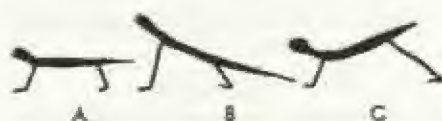


Fig. 555. Diagrams showing the relation of the appendages in a new-born child (A); an adult ape (B); and an adult man (C) (After Wiedersheim.)

quadrupedal position. Such a change of relation during ontogeny is paralleled by the phylogenetic series of primates, as shown diagrammatically in Figure 555.

Embryonically the first part of the budding appendage that shows on the side of the human embryo turns out to be the distal part, that is, the future hand or foot (Fig. 556). This bud soon becomes scalloped, marking the future fingers or toes, and then, after a "web-footed" stage, the separate digits are finally established. Meanwhile the long bones of the arm or leg push out the terminal hand or foot, as the case may be, just as if these extremities were borne upon the end of an extending leverlike handle,



Fig. 556. Successive stages in the development of the human hand. The measurements indicate the sizes of the embryos. (After Retzius.)

(c) **Different Pectoral Appendages.**—The pectoral appendages of fishes are of two general types, represented by the paired pectoral fins of elasmobranchs and the dipnoans. In the former a row of enlarged cartilages, or basalia, at the base of the fin, articulate with the girdle (Figs. 532A and 548). In the dipnoan type, there is a chain of skeletal elements with fin rays equally displayed on either side (Fig. 557).

Various attempts have been made to homologize the skeletons of the paired fins with the bones in the lateral appendages of tetrapods, but without universal satisfaction to comparative anatomists.

Beginning with the amphibians each lateral anterior appendage consists of the following sequence of bones, joined together as a system of levers: a single long bone, the *humerus*, articulating with the girdle; a pair of long bones, the *radius* and *ulna*; primarily three rows of wrist bones, *ossa carpi*; five palm bones, *metacarpalia*; and finally a set of digit bones, or *phalanges*, for each of the five fingers. The typical land appendage is therefore *pentadactyl* (*penta*, five; *dactyl*, digit). In primitive plan there are three wrist bones, or carpals, in the first row, two in the second, and five in the third (Figs. 529 and 558) while the five digits, beginning with the thumb, consist of two, three, four, five, and three phalanges respectively. (See Table X.)



Fig. 557. Diagram of a pectoral fin, "archipterygium," of *Neoceratodus*. (After Galloway.)

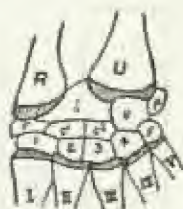


Fig. 558. Carpals of *Sphenodon*, showing two *centrale* bones. R, radius; U, ulna; r, radiale; i, intermediale; u, ulnare; c¹ and c², centralia; 1-5, carpale bones; I-V, metacarpalia; p, pisiforme, a sesamoid bone. (After Baer.)



Fig. 559. Tarsus of a salamander, *Cryptobranchus*. f, fibulare; i, intermediale; t, tibiale; c¹ and c², centralia; 1-6, distal row of tarsals; I-V, metatarsals. (After Wiedersheim.)

In amphibians there are present four fingers instead of five although the number of digits on the hind foot is ordinarily not reduced (Fig. 559). A fusion of the radius and ulna into a single bone, the *radio-ulna*, takes place in anurans, while the middle one of the proximal row of carpal bones, the *intermedium*, is absent.

Among reptiles, *Sphenodon* has two central bones in the wrist (Fig. 558), but only one is common to other reptiles, except crocodiles which have none. The extinct ichthyosaurs and plesiosaurs had a great multiplication of phalanges to sustain their flipper-like appendages, while the fossil

TABLE X. The Homologies of the Girdles and of the Free Appendages

PECTORAL			PELVIC		
Common name	Terms used in Human Anatomy	Terms used in Comparative Anatomy	Terms used in Human Anatomy	Common name	
Shoulder	Scapula	Scapula	Ilium	Hip	
	Coracoid process	Coracoid	Ischium		
	Clavicle	Procoracoid Clavicle	Pubis		
Upper arm	Humerus	Humerus	Femur	Thigh	
Fore arm	Ulna	Ulna	Fibula	Shank	
	Radius	Radius	Tibia		
Wrist	Navicular (Scaphoid)	Radiale	Tibiale	Ankle	
	Lunatum (Semilunar)	Intermedium	Intermedium		
	Triquetrum (Cuneiform)	Ulnare	Fibulare		
	Pisiform	Pisiforme			

Wrist— <i>Cont.</i>		Centrale I Centrale II	Centrale I Centrale II	Centrale I Centrale II	Naviculare	Ankle— <i>Cont.</i>
	Multiangulum majus (Trapezium)	Carpale I	Tarsale I	Tarsale I	Cuneiforme I (Entocuneiform)	
	Multiangulum minus (Trapezoid)	Carpale II	Tarsale II	Tarsale II	Cuneiforme II (Mesocuneiform)	
	Capitulum (Magnum)	Carpale III	Tarsale III	Tarsale III	Cuneiforme III (Ectocuneiform)	
	Hamatum (Unciform)	Carpale IV Carpale V	Tarsale IV Tarsale V	Tarsale IV Tarsale V	Cuboideum	
Palm	Metacarpale I	Metacarpale I	Metatarsale I	Metatarsale I	Metatarsale I	Instep (Sole)
	" II	" II	" II	" II	" II	
	" III	" III	" III	" III	" III	
	" IV	" IV	" IV	" IV	" IV	
	" V	" V	" V	" V	" V	
Fingers	Phalanges (5)	1st row	1st row	1st row	Phalanges (5)	Toes
	" (5)	2nd "	2nd "	2nd "	" (5)	
	" (4)	3rd "	3rd "	3rd "	" (4)	

pterosaurs had an enormously elongated fourth finger to which was attached the stretched sail-like skin, serving as an organ of flight (Fig. 560).

The original quadrupedal character of birds is seen in nestlings, which scramble about the nest, using their undeveloped anterior appendages as legs (Fig. 180). In adult birds complete emancipation of the anterior

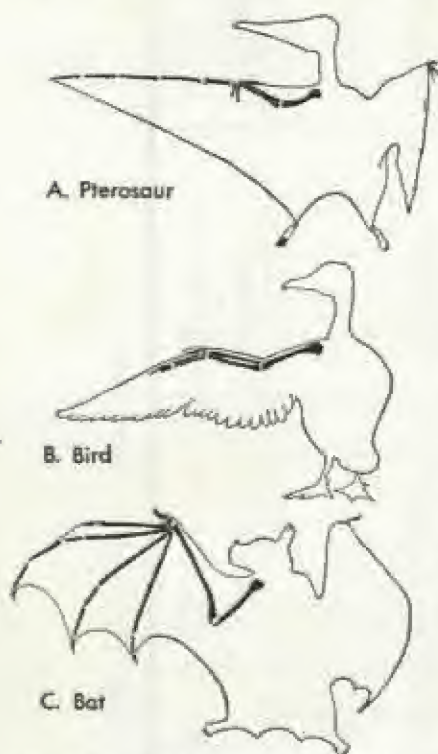


Fig. 560. Three methods of flying with homologous appendages. (After Pander and d'Alton.)

appendages from terrestrial locomotion appears with their extreme modification into wings. Not only are the long bones of the bird's wing much lengthened, but the carpals are compacted together, and the fingers are reduced to three, two vestigial flanking a larger one (Fig. 459), which furnishes a rigid support for the feathers of flight. *Archaeopteryx* points the way that this extreme evolution has taken by the presence of three well developed fingers on each wing (Fig. 47). The tern, *Sterna*, embryonically shows four fingers (Fig. 561), but in all birds the tradition of a pentadactyl ancestry has been quite obliterated, even in their embryonic development.

The anterior appendages of mammals, which have a single, basic plan, exhibit a great variety of modifications, due to the diverse uses to which they are put. Climbing, digging, flying, striking, standing, running, grasping, and lifting are only a few of the many functions that make necessary structural adaptations. Nevertheless, even in the extremely modified flippers of the whale (Fig. 562), it is possible to homologize each of the transformed bones present with those of other mammals.

The human arm is a fore leg which has been freed from the work of locomotion and support, but the inherited system of levers and joints has been diverted to various other uses with conspicuous success. The function of the prehension of food, for example, is no longer confined to the mouth and lips, as in many animals whose arms are still legs, nor are defensive

structures, like horns or fangs, any longer necessary, since the swinging arms take the place of such organs of defence.

The entire arm is pivoted to the pectoral girdle by a ball-and-socket joint which allows great freedom of motion. Other joints between the separate arm bones, while limiting the range of motion in each instance, insure a gain in strength and effectiveness. Thus, at the elbow there is a hinge joint that

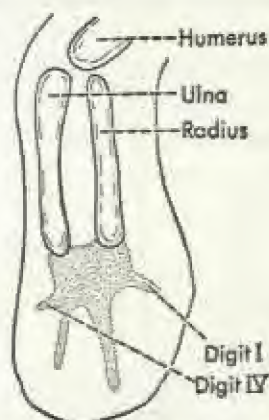


Fig. 561. Fore-limb of an embryo tern, *Sterna*. (After Leighton.)

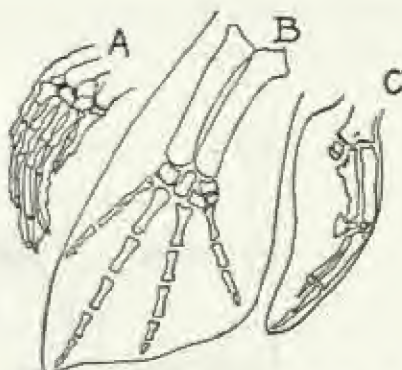


Fig. 562. Flippers. A, sea turtle; B, whale; C, penguin. (After von Hanstein.)

moves in only one plane but which by means of this specialization is rendered all the more efficient. The joints of the wrist and hand are mostly hinge joints, moving likewise in one plane, but the rotation of the radius around the ulna (Fig. 563) brings the hinge action of the hand into any desirable plane.

All of the small wrist bones are irregular, many-sided structures held together by ligaments and so playing upon each other as to allow considerable motion. They fit together as a whole, forming a hollow trough with its convexity on the palmar side of the hand. Across this cavity the *ligamentum carpi transversum* stretches from side to side, and under the bridge thus formed the tendons, blood vessels, and nerves that supply the fingers go in safety.

The articulations of the wrist bones, as well as the other bones of the arm, are shown diagrammatically by dotted lines in Figure 564. It will be seen from this diagram that the entire hand is hung upon the radius which is enlarged at the carpal end to receive it. Although the radius takes some part in the articulation of the forearm to the humerus at the elbow joint, this function is mainly accomplished by the ulna, which is consequently

enlarged at that end. Such an arrangement makes it possible for the distal end of the radius bearing the hand to rotate freely in a half circle, carrying the complex hand bones with it.

When the radius and ulna are parallel, the hand is palm up in an attitude of supination. This is called *supination*. The opposite attitude of *pronation* occurs when the radius and ulna are crossed and the palm of the hand is turned down (Fig. 563). In all mammals except primates the radius and ulna remain permanently crossed.

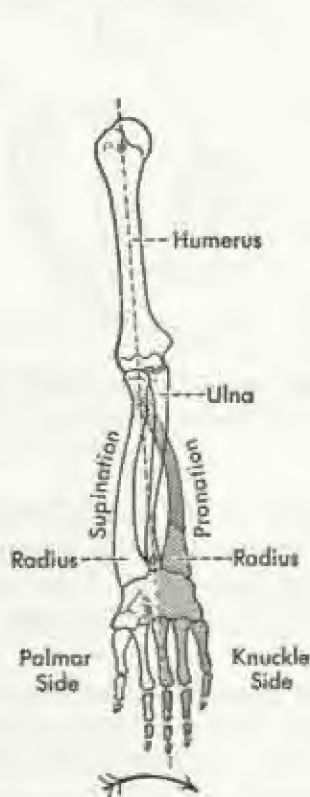


Fig. 563. Diagram showing the relative positions of the radius and ulna in pronation and supination. (After Heitzmann.)

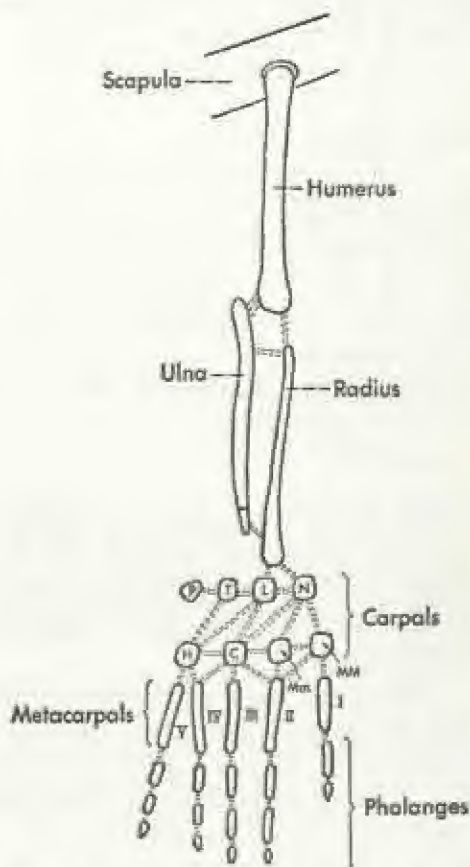


Fig. 564. Diagram showing how the hand is hung upon the radius, and the articulations (dotted lines) of the wrist.

Although *centrale* bones occur in most monkeys and some apes, they were not known in man until in 1874 they were discovered by Rosenberg in the human embryo. Their disappearance during the third fetal month is due to their fusion with other wrist bones.

Four small *sesamoid bones*, embedded in tendon, are regularly present on the palmar side of the hand. Two are at the metacarpo-phalangeal joint of the thumb, while one each is at the metacarpo-phalangeal joint of the index, and of the little finger. Frequently still other sesamoid nodules are found at the finger joints. A careful and extended study of a large series of human wrist bones, such as that made by Pfitzner, has revealed the presence in various situations of a great number of supernumerary wrist bones aside from the regular sesamoid bones. Figure 565 is a composite diagram from Pfitzner, showing the location of fifteen extra bones found in different human wrists, indicating that this region is still being extensively molded by evolutionary factors.

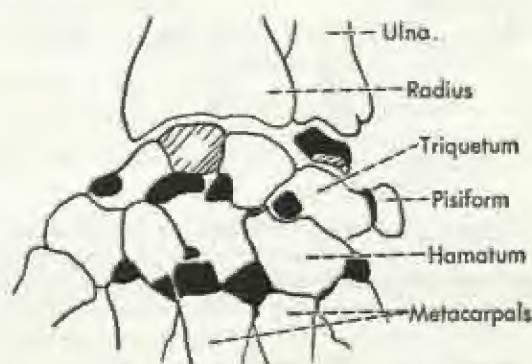


Fig. 565. The volar aspect of the human wrist showing (in black) where extra wrist bones have been found in various individuals. (After Pfitzner.)

Syndactylism, or the growing of fingers together, *brachydactylism*, in which one phalanx of each digit is missing, and *polydactylism*, or the addition of extra fingers, all occur occasionally in man as well as in other vertebrates.

(d) **Different Pelvic Appendages.**—The sequence of bones in the pelvic appendages is homologous with that of the pectoral appendages, as shown in Figure 529 and in Table X, in which the synonyms of the names employed for the various parts are included. In birds and mammals the *patella*, a sesamoid ossification embedded in the extensor tendon over the knee, is generally present (Fig. 581), and a similar sesamoid, the *brachial patella*, rarely occurs at the elbow joint.

In general the chain of levers which the leg bones form acts as a "pusher" in locomotion, while that of the anterior appendage serves as a "puller" (Fig. 566). This is true both for quadrupeds progressing on the ground and for climbers in trees.

Elbows are bent backward and knees forward in quadrupeds, thus centralizing the long bones of the appendages under the body. The push or kick of the hind leg is more effective in locomotion than the pull of the front leg. It is the idea of the wheelbarrow rather than the drag-cart for carrying a load easily.

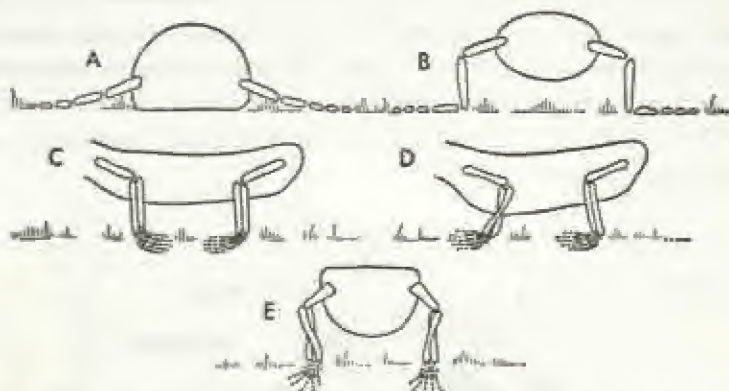


Fig. 566. Diagram illustrating evolution of the limbs of tetrapods. A, anterior view of early stage when limbs stick out laterally and ventral surface of body rests on ground; B, later stage when body is lifted from ground, but limbs project to the side; C, hypothetical condition in which hind-limb is rotated forwards from acetabulum and fore-limb rotated backwards from glenoid cavity, but fore-arm bones are not crossed; D, actual condition in which radius has crossed over ulna when fore-arm rotated forwards; E, anterior view of stage shown in D. (After DeBeer.)

The differentiation between the anterior and posterior appendages in birds is very great (Fig. 422). The legs assume the entire support of the body upon the ground, having become modified accordingly. The fibula becomes reduced and the several metatarsals fuse into a single bone, while the tarsals are reduced in number and solidly joined to other skeletal parts in the interest of increased firmness and strength, the proximal row fusing with the distal end of the tibia, and the distal row with the metatarsal, which brings the ankle joint between two rows of tarsal bones as in many reptiles.

The arrangement of levers in the leg of a bird combines the ability to walk and run with the possibility of sudden elevation in order to "hop off" in aviation. This latter accommodation is attained through the angle that the femur normally assumes with the tibiotarsus when not in flight. It will be seen (Fig. 567) that a bird is "sitting down" while it is still standing up, since the knees are directed forward horizontally, as in a sitting man. This

position enables it, by straightening the legs suddenly, to rise enough from the ground or the perch to take to the air successfully. When a bird "squats" (Fig. 567B), the leg bones jack-knife together, thus pulling the tendons attached to the toes taut and clinching the phalanges around the perch. To unlock the foot it is necessary for the body to be raised, thus straightening the leg and loosening the tendon which has been pulled tight over the ankle by the downward weight of the body in perching. When a bird perches, therefore, it is automatically locked for the time being upon the perch and can go to sleep without fear of falling off.

Among mammals the ankle joint is never between the rows of tarsal bones as in the reptiles and birds.

The difference between the hand and foot of man is greater than in any other animal. In apes the functions of grasping and support are partly shared by both the hand and foot (Figs. 568 and 569), whereas in man these two lines of activity have become entirely segregated, although some individuals have the ability to flex the toes enough to grasp awkwardly such an object as a handkerchief as well as to pick it up.

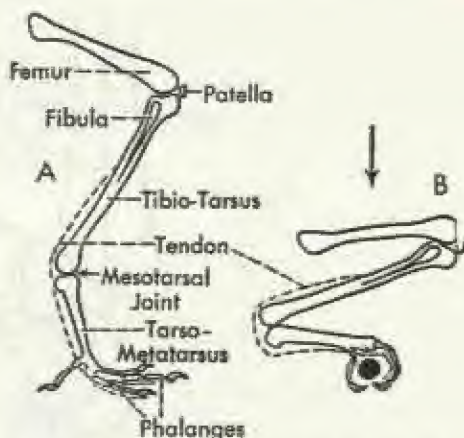


Fig. 567. The perching mechanism of a bird. A, standing; B, perching.



Fig. 568. The palm of the hand of an orang-utan, showing the poorly opposable thumb. (After Primrose.)



Fig. 569. The sole of the foot of an orang-utan, showing the thumblike big toe. (After Primrose.)

The ankle bones, which must support the weight of the body, form at least one half of the entire foot (Fig. 570), while the wrist bones do not make up more than one sixth of the grasping hand with its long fingers (Fig. 571). The longest toe is about one fourth the length of the foot while the longest finger is fully half the length of the hand.

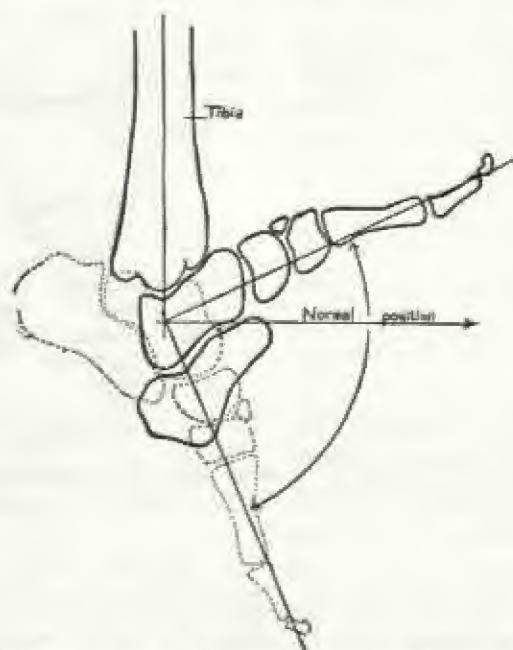


Fig. 570. Diagram showing the normal extent of the hinge movement allowed by the ankle. Compare with Figure 571.

The human foot is arranged practically at right angles to the leg (Fig. 570), while the hand hangs straight down at the end of the arm, making an angle of 180 degrees (Fig. 571). Moreover, the bending of the wrist towards the palm side is easily accomplished through an arc of at least 90 degrees, while the corresponding movement of the foot at the ankle is made with difficulty through a third of that distance, as shown diagrammatically in Figures 570 and 571.

On the other hand the swing away from the natural position in the opposite direction, which raises the foot up on the toes but accomplishes nothing useful for the grasping hand, is much freer and can extend through a larger arc in the case of the foot than in the hand. Rotation, which is easily accomplished by the hand by means of the way that the radius and ulna are hung from the humerus, is possible only in a slight degree in the

foot. Since the tibia does not rotate on the fibula as the radius does on the ulna, the lateral swing of the big toe from right to left and back again is consequently limited.

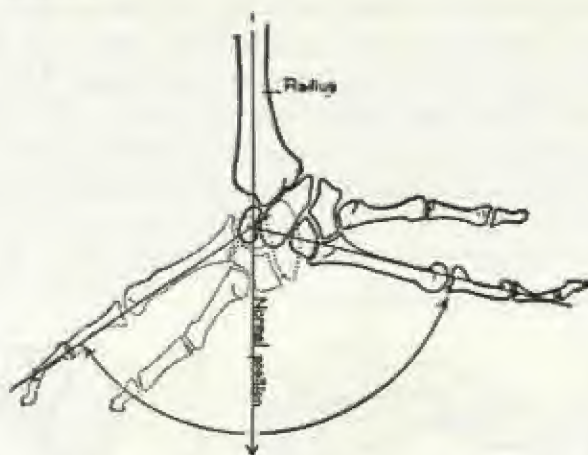


Fig. 571. Diagram showing the normal extent of the hinge movement by the wrist. Compare with Figure 570.

In hoofed animals like the cow and horse, the specialization of a supporting leg and foot has gone much further than in man with the result that the rotary movement is entirely lost.

The human foot is *plantigrade* (Fig. 573), having not only phalanges and metatarsals, but even some of the tarsals, in contact with the ground. Birds and fissipede carnivores, for example cats and dogs, are *digitigrade* (Fig. 182), because the ankle is lifted off the ground, while ungulates are *unguligrade*, that is, elevated on the tips of toes terminating in hoofs (Fig. 524). The unguligrade tapir of South America rests on the ends of four toes on each front foot and three on each hind foot. The pig walks on two toes with two degenerate toes hanging on either side (Fig. 572), that make an imperfect impression only when the animal walks over soft or muddy ground into which the feet sink. Artiodactyls generally are two-toed with the other toes in various degrees of degeneration, while perissodactyls, like the horse, are reduced to standing on the tip of a single toe on each foot.



Fig. 572. Evolution of artiodactyl foot. (After Flower.)

The horse's ancestral gallery of family portraits shows all intermediate degrees of evolution from the five toes of *Eohippus* to the single toe of the modern horse. Flat-footed man would have a long road to travel before he reached the extreme stage of pedal evolution attained by the horse.

The bones of the human foot are arranged in the form of two arches, which act as springs or shock absorbers in locomotion. They also protect from pressure the nerves and blood vessels of the sole. The *long arch* rests upon the ground both at the heel and upon the ball of the foot or, in terms of the skeleton, upon the posterior end of the *calcaneus* and the distal ends of the *metatarsals* (Fig. 573). It has for a keystone the *talus*, or *astragalus*, which bears the weight of the body and is the only bone of the foot that articulates with the shank of the leg.

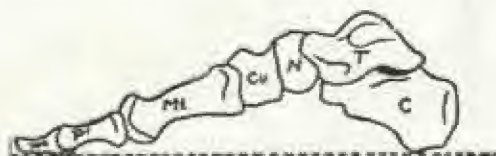


Fig. 573. The long arch of the foot. c, calcaneus; t, talus; n, navicular; cu, cuneiforme; mt, metatarsal; p¹ and p², phalanges.



Fig. 574. A cross section through the middle of the foot, showing the transverse arch. (After Rauber.)

The smaller *transverse arch* (Fig. 574) extends from side to side through the distal ends of the sprawling metatarsals. In standing still the weight of the body rests principally upon the long arch, but when the center of gravity is thrown forward as in walking, the weight of the body shifts temporarily to the transverse arch every time one comes up on the ball of the foot or the toes. Then with the weight thrown forward the transverse arch tends to flatten, allowing the toes to grip the ground, and to pull the body forward effectually. This happens most perfectly in the case of the unrestricted bare foot that is not crowded into an unyielding hooflike shoe. It is obvious that high-heeled shoes throw the standing weight forward so that the long arch does not function properly, and the transverse arch, which should be reserved for springy locomotion, gets more than its share of burden-bearing. Any arch resting on two pillars spreads its weight over a larger area, making a more stable foundation than would be the case with a single column supporting the same amount of weight. The long arch of the foot is tipped up on end by the high-heeled shoe so that the line of gravity runs mostly through only one pillar instead of through two, in consequence of which it no longer functions as an arch, because the mechanical advantages which an arch possesses are thus sacrificed.

The awkwardness exhibited in walking on stilts or crutches is partly due to the absence of the double point of contact with the ground that is furnished by the arch. Again, tight shoes across the toes, that do not allow the transverse arch to spread properly in walking, prevent the proper pull on the ground by the toes and add greatly to the mechanical difficulties of locomotion. Human feet have never quite recovered from the effect of having the body tipped up on end with the entire responsibility of its support thrust upon them. In the evolutionary time at their disposal they have developed the best they could with the inherited materials with which they had to do, but it must nevertheless be confessed that the result is as yet only a makeshift foot. The various foot troubles of man are an eloquent confirmation of this statement.

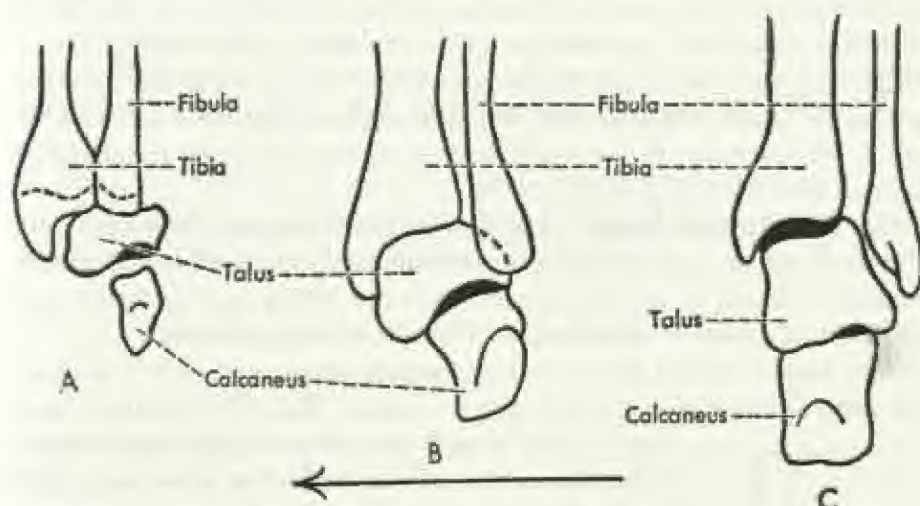


Fig. 575. The heel, as seen from behind. A, a chimpanzee; B, an Australian bushman; C, a Caucasian. The fibula plays a decreasing rôle, while the calcaneus tends to shift in the direction of the arrow. (After Wiedersheim.)

Man needed to have a considerable part of the foot bent at right angles to the leg so that it would come into contact with the ground and thus prevent the upright body from tipping over forward. At the same time a part of the foot, the *heel*, had to be detailed to project in the other direction to prevent tipping backward.

The flatness of the foot, however, necessitated the formation of the arches just described which entailed adjustments in the case of every bone of the foot. That these adjustments at present are far from perfect is at once apparent when the arrangement of the bones of the foot is carefully scruti-

nized. The ankle bones, for example, together resemble a cairn of irregular stones piled one upon another, on the top of which is precariously balanced the weight of the body. Furthermore, the big *calcaneus*, or heel bone, is not squarely placed directly under the line of the center of gravity as a foundation stone should be, but is rather to the outside of this plumbline. That it is gradually being shoved under into a mechanically better position is shown in Figure 575, where is pictured the less satisfactory adjustment in the case of a primitive Australian and the still more primitive bow-legged ape. This outside lateral position of the calcaneus, like the run-over heel of a shoe, causes the weight of the body to veer over toward the inner or big-toe side of the foot. The long arch, moreover, is considerably higher and more effective on the inner side of the foot than it is on the outer, as any print of the normal bare foot in the sand demonstrates. The result is that the big toe is becoming larger while the little-toe side of the foot is degenerating.

The big toe is said to be relatively somewhat longer in the human male than in the female which, if true, would be evidence that the male, with his feet if not his head, has traveled a little further along the evolutionary highway than the female of the species.

(c) **The Human Hand.**—The human hand takes an important part with the large brain in placing man triumphant at the head of the animal creation. Without its aid the arts and sciences, which are the flower and expression of human civilization, would not have been possible.

The hand is first of all a universal grasping device, mounted on a movable arm, that can hold a tool or grip a weapon (Fig. 576). Without such artificial aids as tools and weapons man would still be a beast whose only substitutes for hands are specialized organs that are adapted for a narrow range of use, as for example, the goring horns of a bull or the chiseling teeth of a beaver. Once the hand is present that is capable of grasping artificial aids, the invention and utilization of all sorts of accessory devices goes forward with leaps and bounds, entirely unparalleled in the slow evolutionary process of adaptation by natural selection of bodily structures. As an evolutionary resource such a short cut to efficiency is an incalculable advantage to its possessor. Aside from man probably only the higher apes among animals make any attempt to use even so simple a tool or weapon as a stone or a stick. The idea of fashioning anything to be held in the hand for any purpose whatsoever belongs entirely to man.

The absolute dependence of man upon the opposable thumb, which has



Fig. 576. The opposable human thumb.

been significantly called "Wotan's finger," and the grasping hand that results is the key to most human activities. The thumbless spider monkey (Fig. 577) is only partly compensated by its prehensile tail.



Fig. 577. Thumbless hand of a spider monkey, *Ateles*. (After Haacke.)

What laborer works without his hands? What artisan, even in the "machine age," can produce anything without in some stage of the process "fingering" it? The artist who creates a painting or a statue must hold brush or chisel. Even the prize-fighter clenches his fist with its tightly opposable thumb. The mechanical performance of all writing or printing, with everything that this means in the recording and communication of ideas, is primarily thumb-and-finger work, and the same is true of most of the daily activities that make up human life. The common phrase "he had a hand in it," expresses exactly and literally the part dominant man has taken and continues to take in the world's affairs.

Production of Motion and Locomotion—Muscles

I. IN GENERAL

Muscles are characteristic of animals rather than of plants. When danger is near animals may make an escape but plants must stand still wherever fate has placed them. Animals employ muscles in the daily business of food-getting, and also by means of them go afield in quest of mates. Muscular movements, which play an important part in courtship, enable animals to exercise some degree of choice in the altruistic matter of reproducing their kind. With non-muscular plants, on the other hand, "forced marriage" without choice, and by some outside agency such as wind, water, or officious insect, is the universal rule.

Not only in *locomotion*, or bodily movement from place to place, but also in *motion*, or the movement of the organs of the body, do muscular animals have a great advantage over plants, for plants must depend upon such physical agencies as wind, internal turgor, or unequal growth in order to effect the rustling of their foliage, twining of their tendrils, and closing their leaves in "sleep."

From the insignificant flatworms up to man evolutionary development is particularly mirrored in the musculature, which has dragged with it all the other systems. The bobolink on the wing over a sunny meadow sings a cheerful hymn of praise to the muscles, and conquering man by means of muscles is able to go forth to the four corners of the earth.

By the agency of musculature man lies down, stands up, sits, walks, runs, jumps, creeps, dances, skates, skis, writes, drives, paints, makes a machine, and plays a violin. What other animal can do all this!

The actions of animals, which "speak louder than words," are brought about by the triple agency of nerve, skeleton, and muscle. Of this trinity of parts the muscles, or "flesh," constitute the greatest bulk, making up in

man approximately half of the total weight. Although the skeleton, or scaffolding, is the primary factor in determining the form of the body, the muscles that drape the skeleton are chiefly responsible for the characteristic contours which give it grace and beauty of outline.

It is very essential for the surgeon to possess detailed knowledge of the separate muscles of the human body. Consequently careful training in *Myology*, or the science of muscles, is a part of the indispensable discipline that every well-equipped medical student must undergo, and this knowledge can be attained only by careful and repeated dissections, rather than by reading descriptions of muscles in books. A superficial comparative survey of the muscular system in different vertebrates, which is all that will be attempted in this chapter, may, however, be profitably undertaken by any student, whether or not he is looking toward a medical career.

II. MUSCULAR ACTIVITY

Muscular activity, or the way animals expend their energy, has its morphological basis in cellular units, which, unlike inorganic substances, possess the power to increase with use. Muscle cells, although presenting nothing fundamentally new in cell structure, are specialized in the matter of *contractility*, which is one of the universal properties of protoplasm.

Elastic *myofibrils*, that shorten in only one direction, appear within the muscle cell, and these are capable of causing movement not only within the cytoplasm of the muscle cell itself, but also outside of it, thus effecting both motion and locomotion.

Muscular movement is always the result of *muscular contraction*. When, for example, a leg is bent by shortening one set of muscles, it is restored to its original position not by the relaxation of these muscles but by the contraction of an antagonistic set on the other side of the leg (Fig. 578). Usually the group of muscles that flexes, or brings the appendages close to the body, is stronger than its opponents. In the chewing muscles of the jaws those that effect the bite are stronger than their opponents which open the jaws for another bite.



Fig. 578. Antagonistic muscles of the human leg. (After Mollier.)

Whether this fundamental difference in opposing muscles has any deep evolutionary significance or not is open to speculation, though natural selection is always on the lookout for whatever may contribute to individual preservation. In any case the centralized drawing in of the arms by flexion is better adapted for defensive purposes than the opposing gesture of wide-flung extension of the appendages.

Aside from accomplishing countless necessary movements of different parts of the body, and serving as the engine of propulsion for the animal machine, muscular activity contributes in a variety of ways to the welfare of the animal organism. For example, the exercise of the muscles constantly changes the character of the blood and lymph, since more carbon dioxide is given off from the blood during exercise than at other times; vascular congestion is decreased by the muscular dilation of the arteries, and at the same time the ventilation of the lungs is increased; the lymph flow is promoted; peristalsis is stimulated; and the heart is trained not only to continuous performance but to meet emergencies.

The muscles of the living body are never entirely relaxed, but maintain a *tonus*, that is, a condition of balanced tension between opposing sets. In standing erect there is ceaseless employment of opposing muscles, and when the body wall is pierced by a bullet the resulting hole is more slitlike than round, showing that the muscles involved are always somewhat taut even when not effecting motion. Considered in all aspects the muscular work done by an ordinary ambulatory human being during a lifetime amounts to a dizzy total.

The duration of contraction and the interval elapsing before the next contraction vary greatly in the muscles of different animals. It has been reckoned, for example, that the duration of contraction in cold-blooded turtles and frogs is one second and one fifth of a second respectively, while in man it is one tenth of a second. A violinist can make ten muscle movements per second in executing a trill with his fingers, but a buzzing house fly has a record of 330 muscular movements per second. What a Paganini a fly would make!

Fatigue following muscular activity results from the release of lactic acid into the blood stream. Muscles always react in the same manner, by a change of form accompanied by the release of lactic acid and the production of heat, regardless of the category into which the stimulus applied may fall, whether it is nervous, chemical, physical, or mechanical. Consequently a muscle cannot be described as exclusively a thermo-dynamic, a chemo-dynamic, or an electro-dynamic apparatus.

III. MUSCLES AS TISSUES

Muscles may be considered from the point of view of tissues or of organs.

There are three sorts of muscle tissues (already briefly described in Chapter VII as *smooth*, *striated*, and *cardiac*), which differ from each other in origin, histological appearance, physiological action, and distribution. Each muscle cell connects with a nerve ending that controls its behavior.

Smooth muscle cells, which have to do with the events that go on inside the body, are derived from mesenchyme, are comparatively short, have a single nucleus (Fig. 92A), and are frequently isolated or combined in thin sheets. For example, every hair is provided with an individual pomade tube in the form of a sebaceous gland, administered by its own private smooth muscle in the skin (Fig. 158) which makes the hair "stand on end" and also presses the secretion from the gland.

In the walls of blood vessels smooth muscle cells are arranged mainly in circular fashion, thus decreasing the bore of the passage-way upon contraction, while the enlargement of the lumen is brought about by blood pressure. They occur not only in the walls of blood vessels and in the skin but also in the walls of the digestive tract, the urogenital passages, and ducts of various kinds, thus forming parts of other organs rather than whole organs in themselves. Since they are supplied from the autonomic nervous system they are comparatively slow in action and are involuntary.

Striated muscle fibers (Fig. 92B) are elongated cells which constitute most of the musculature of the body, particularly the muscles with skeletal connections. They differ from smooth muscle cells in at least the following points, being (1) anatomically more complicated; (2) embryonically younger; (3) connected with the voluntary nervous system and consequently under the control of the will; (4) quicker in action; (5) more easily tired; (6) less stretchable; and (7) weaker in effect. The enormous power of extension of the smooth muscles is shown in the great capacity for dilation possessed by the stomach, for example, or the urinary bladder, while the remarkable strength exerted by them in contrast to skeletal muscles is demonstrated by the extraordinary expulsive power exerted by the walls of the gravid uterus. In general the strength of striated muscles is proportional to their thickness, while the degree of contractility is dependent upon their length.

Cardiac muscle cells or fibers, which are intermediate between smooth muscle cells and striated muscle fibers, are of mesenchymal origin, being modified from the tunica media of an embryonic blood vessel. They are short multinucleate structures, usually branched or anastomosing together

and showing faint striations (Fig. 109). Unlike true striated muscle cells, they are involuntary in action. They occur in the walls of the heart, as well as of the pulmonary arteries and veins, and also in the roots of the aorta.

IV. MUSCLES AS ORGANS

While smooth and cardiac muscle cells form mainly tissues, which are parts of various organs, striated muscle cells combine to form organs with more or less morphological and physiological unity. Connective tissue sheaths, while making possible the action of a muscle as a whole, separate single parts of muscles so that their identity is not always easy to determine. A further complication is encountered by the comparative anatomist in determining the homologies of muscles in different vertebrates, since the names applied to them are borrowed from human anatomy, although frequent changes in function, liable to throw the investigator off the evolutionary track, have occurred.

Anyone with experience in the dissecting rooms of a medical school is well aware of the difficulty in trying to make a dissection invariably meet the expectation of the manual, for there is great individual variation in separate muscles, and even in homologous muscles on the two sides of the same individual. As a matter of fact muscles are not nearly as conservative as bones, teeth, and nerves. There is consequently a difference of opinion as to how many muscles are to be accounted for in man. One authority lists 639, of which 5 are unpaired and 317 are paired, with the following distribution: head, 53; neck, 32; back, 180; breast, 54; belly, 15; legs, 124; arms, 98; and viscera, 83. Testut has written an impressive tome of 900 pages, *Les anomalies musculaires chez l'homme*, 1884, which deals mostly with variations found in the muscles of the human body.

None of the paired muscles oversteps the midline which divides the body into right and left halves. It is not unusual, however, for a pair of muscles to develop more on one side than on the other, resulting ordinarily in right and left handedness. Statistics show that nearly 96 per cent of humankind are "righthanded," and consequently we may be said to have a righthanded civilization. This is recognized in the way we make our screws, scissors, fire-arms, watches and clocks, buckles and buttonholes, coffee mills and hand-organs, violins and flutes, and in the way we shake hands. Some famous lefthanders who made a notable impression in a righthanded world are Leonardo da Vinci, Michelangelo, Holbein, Menzel, and Napoleon.

The *biceps muscle* may be taken as a typical representative (Fig. 579) of a muscle. It consists of an enlarged middle portion, the *belly*, with taper-

ing ends, and is surrounded by a connective tissue sheath which at the ends becomes continuous with *tendons*, that in turn merge into the *periosteum* ensheathing the bones, thus securing anchorage for the muscle. One end of the muscle, the *punctum fixum*, where it is attached to the most stationary part of the skeleton, is the *origin*. The other end, the *punctum mobile*, where it connects with the part of the skeleton which it moves, is the *insertion*. Upon the contraction of a muscle the insertion is always pulled towards the origin. There may be several insertions, as in the *serratus* muscles along the back, or there may be more than a single origin, for example, in the biceps there are two present, giving it the name "biceps."

Sometimes, as in the *trapezius* muscle, which moves the head and shoulder, the *punctum fixum* may become the *punctum mobile*, according to the movement to be effected.

The wide range of variation in form (Fig. 580) is a necessary adaptation in the accomplishment of different movements. The original form of embryonic muscles shows sheets of fibers, or *myotomes*, extending between partitions of connective tissues, similar to the arrangement of muscles on the sides of the body of a fish. Out of this primitive alignment modifications are initiated (1) by delamination, or splitting flatwise; (2) by splitting lengthwise; (3) by proximo-distal division; and (4) by various degrees of fusion.

The shapes that muscles assume also exhibit a great variety. The word itself (*musculus*, little mouse) indicates an originally rather compact form that has undergone much adaptive streamlining in successfully accomplishing different movements. The muscles of the limbs are often fusiform, like the shape of a single smooth muscle cell, since this type is less bulky for the amount of muscular tissue involved than some other shapes. Triangular muscles appear where there are broad origins and narrow insertions, such as are found in the *deltoid* and *pectoralis* groups. Sheet muscles occur in situations like that occupied by the *diaphragm*, where the work to be performed is best served by this morphological form.

It is not always easy, as already pointed out, to delimit a muscle, because of the changes brought about through functional necessity. The best criterion, however, for homologizing a muscle is its nerve supply. A nerve once assigned to do duty with a particular muscle follows it through all its

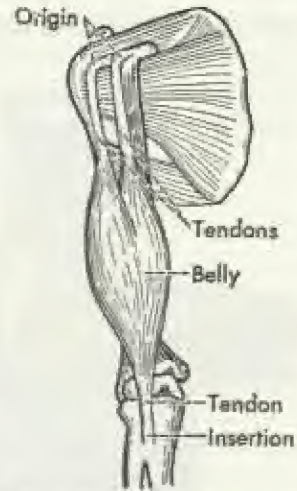


Fig. 579. The biceps muscle, showing origin and insertion. (After Mollier.)

vicissitudes, just as a faithful dog, trotting behind its master, serves to identify him, regardless of the different costumes or disguises which the master may assume.

A striking illustration of the constancy of nerves to transforming muscles is furnished by the *phrenic nerve* that supplies the diaphragm, which is a migratory muscle laid down originally far anterior in the neck region. With



Fig. 580. Superficial muscles of the back. (After Morris.)



Fig. 581. The tendon of Achilles, in black, showing how the work which muscles do may be applied at a point some distance from the muscle itself.

the backward shifting of the heart the diaphragm finally assumes an abdominal position remote from the neck, yet the phrenic nerve, although made up from the third, fourth, and fifth cervical nerves, goes out of its way to retain connection with it and to proclaim its origin.

As already indicated *tendons*, or sinews, are means by which muscles are attached to bones, and in this capacity they serve a double purpose. In the first place they enable soft, delicate, contractile muscles to gain a firm, tenacious grip upon solid skeletal parts, whereby motion may be effected.

They also enable large muscles that make up the bulky part of the body to be packed in out-of-the-way situations, sometimes at considerable distances from the work to be performed, where they will not interfere by their bulk with the free movement of the joints. The "tendon of Achilles" (Fig. 581), like the electric cable that transmits power generated at Niagara Falls to industries in the city of Buffalo, for example, is the most efficient arrangement for the ankle to have, because muscles connected with it are largely concentrated out of the way at the "calf of the leg," rather than around the ankle itself, where they would interfere with the freedom of the movements they are detailed to perform.

Muscles generally are encased in connective tissue sheaths, or *epimysium*, which are more or less continuous by means of connecting tendons with similar periosteal sheaths surrounding skeletal parts. Connective tissue elements, *perimysium*, also extend even between groups of muscle fibers themselves, separating them into irregular bundles, or *fasciculi*.

Sometimes ossifications occur, embedded within tendons at points of friction. These are called *sesamoid bones*, the most conspicuous example being the knee-cap, or *patella* (Fig. 581), mentioned in the preceding chapter. Sometimes an entire tendon ossifies, as may be seen on the sides of a turkey's "drumstick."

The topographical relationship of neighboring muscles to each other and to the bone foundation which they surround is typically indicated by Figure 582, in which is represented a diagrammatic cross section of a cat's front leg above the elbow. Blood vessels and nerves are shown between the muscles.

Movements brought about by muscles are described by a variety of terms, including: flexion, extension, adduction, abduction, elevation, depression, rotation, constriction, and dilation. *Flexion* is the bending of a part, as of the arm at the elbow, while *extension* is the opposite action, the bringing of two parts into line with one another, as in straightening the arm. *Adduction* is the swinging of an arm or leg ventrally, usually toward the median plane; the opposite action, *abduction*, is the swinging of the appendage dorsally. *Elevation* is the pulling of a part dorsally, for example the "drawing back" of the shoulder-blade (scapula) or the raising of the lower jaw to close the mouth; *depression* is the drawing of a part ventrally and includes the "dropping" of the lower jaw in opening the mouth. *Rotation* of parts on one another includes *supination*, or the turning of the palm of the hand to face upward, and *pronation*, or the turning of the palm to face downward. *Constriction* is the function of sphincters, such as those which close the mouth or anus or reduce the size of the pupil of the eye; *dilation* is the opposite action, by muscles which enlarge the opening.

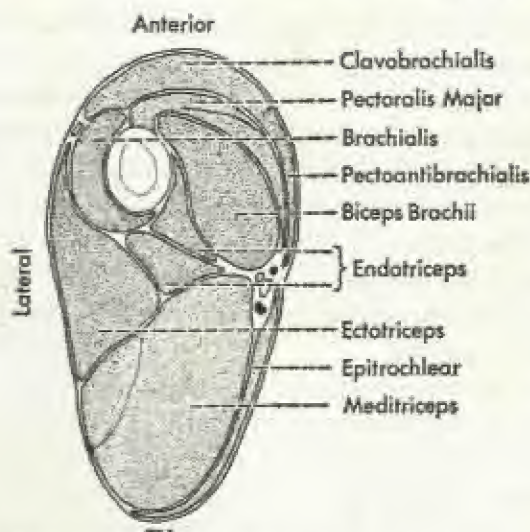


Fig. 582. Muscles of the front leg of the cat, in cross-sectional view. Proximal cut-surface of the right leg, or distal cut-surface of the left. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

V. EMBRYOLOGY OF MUSCLES

When mesoderm enters the scene in vertebrate development, there is much more of it along the dorsal side of the embryo, *epimerically*, than on the ventral side, *hypomerically* (Figs. 115 and 116). This distribution is not true of invertebrates, such as annelid worms, in which the mesoderm is about equally distributed all around the body. The reason for the excess of mesoderm along either side of the notochordal level in vertebrates is that this region, after giving off dermatomes and sclerotomes, becomes the *myotomes*, or *muscle plates*, from which nearly all of the striated muscles of the body are derived. While the major parts of the myotomes remain alongside the developing vertebral column, portions grow ventrally into the region between the parietal mesoderm of the hypomere and the integument until only a thin sheet of connective tissue, the *ventral septum*, lies between the ventral ends of the myotomes derived from opposite sides of the body.

During these embryonic changes the muscle cells, originating in the epimeric myotome, become rearranged so that their long axes come to parallel the long axis of the body, while between the myotome masses are developed mesenchyme partitions of connective tissue, *myocommata*, to which the muscle fibers are primarily attached. The end result, as well shown in amphioxus (Fig. 13), is a series of <-shaped *muscle plates*, extending along the sides

of the body and separated from each other by myocommata. These muscle plates are destined to form the axial muscles of the body from which the appendicular muscles secondarily bud forth, as soon as the skeletal parts of the appendages themselves arise and furnish a foundation for muscular attachment.

Even in man (Fig. 583) the embryonic arrangement of body muscles is metameric at first, from which primitive arrangement the complications of adult musculature are subsequently derived.

Involuntary muscles generally are mesenchymal in origin, but the muscles of the iris, which control the size of the pupil of the eye, are ectodermal.

VI. KINDS OF VOLUNTARY MUSCLES

In *The History of the Human Body*, 1923, by H. H. Wilder an excellent analysis of the comparative anatomy of the muscular system classifies the voluntary muscles under three groups, namely, *metameric*, *branchiomer*, and *integumental*.

The *metameric* group, which includes the axial and appendicular muscles, in reality takes in most of the muscles of the body.

*Branchiomer*ic muscles are associated with the primitive splanchnocranium and its derivatives, while the *integumental* group consists of muscles that have split off secondarily from the two preceding groups, and have taken up major associations with the integument rather than the skeleton.

The voluntary striated muscles will be briefly considered in the following order:

1. Metameric
 - (1) Axial
 - (a) Head
 1. Eyeball
 2. Hypoglossal

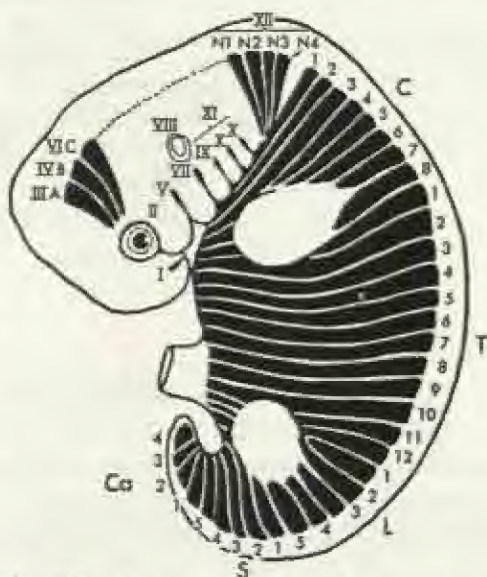


Fig. 583. Scheme to illustrate the disposition of the myotomes in the human embryo. A, B, C, the first three cephalic myotomes; N, 1, 2, 3, 4, last persisting cephalic myotomes; C, T, L, S, Ca, the myotomes of cervical, thoracic, lumbar, sacral and caudal regions. Roman numerals refer to cranial nerves. (After Cunningham.)

- (b) Trunk
 - 1. Ventral
 - 2. Dorsal
- (c) Diaphragm
- (2) Appendicular
 - (a) Extrinsic
 - (b) Intrinsic
- 2. Branchiomic
 - (a) Vth cranial nerve group
 - (b) VIIth cranial nerve group
 - (c) IXth cranial nerve group
 - (d) X-XIth cranial nerve group
- 3. Integumental

1. Metameric Muscles

(1) **AXIAL MUSCLES.**—Primarily the *axial muscles*, which are the first to appear both embryonically and phylogenetically, are arranged with regularity in myotomes down the side of the body, fitting into each other like a nest of spoons. There may be sixty or more pairs of these myotomes in amphioxus, varying somewhat in symmetry on both sides of the body. When their longitudinal fibers contract, they exert a pull upon the myocommata that separate the myotomes from each other, and secondarily by this means upon the stiff notochord, the outer sheath of which is continuous with the myocommata.

The myotomes are all practically alike, though diminishing in size toward the tail. With the advent of the head in fishes the first real modification of this primitive form of musculature appears in the fusion of some of the myotomes and a consequent breaking up of the regular metamerism of the axial muscles.

(a) **Head.**—Skull muscles are few in number, being reduced in correlation with the increasing absence of movable skeletal parts in this region. The three anterior pairs of myotomes (Fig. 583) become the six pairs of muscles that move the eyeballs within their sockets (Fig. 584). As these muscles are quite conservative, they exhibit only minor modifications throughout the vertebrate series. The most anterior identifiable myotome, which is supplied by the third cranial nerve (oculomotor), gives rise to the *superior rectus*, the *internal rectus*, the *inferior rectus*, and the *inferior oblique muscles*.

The myotome next posterior, which is supplied by the fourth cranial nerve (trochlear), becomes the *superior oblique muscle*, and is followed, after a gap that probably represents a missing myotome, by one supplied by

the sixth cranial nerve (abducens), that is responsible for the *external rectus muscle*, and also the *retractor bulbi* which first appears in amphibians.

Incidentally this latter muscle has a unique function, for in addition to pulling down the eyeball of a frog, which pops up like a jack-in-the-box as

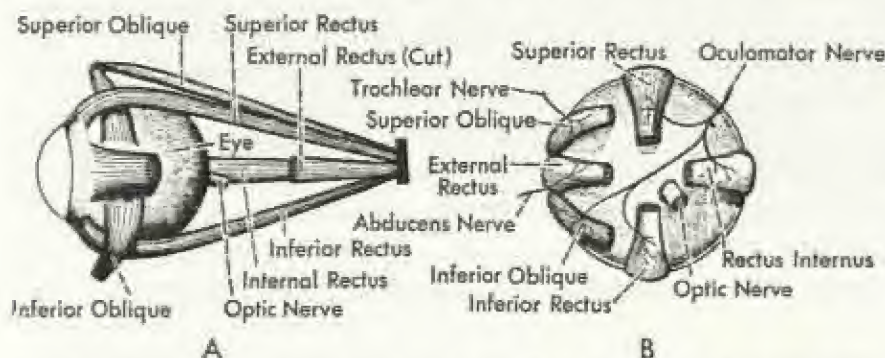


Fig. 584. Extrinsic muscles of the left eyeball of man. A, side view; B, viewed from behind. (From Neal and Rand, *Comparative Anatomy*, copyright 1936, by permission of P. Blakiston's Son and Company, publishers. After Warren and Carmichael.)

soon as the muscle is relaxed, the *retractor bulbi*, in the absence of a hard palate, enables the eyeball to aid in gripping whatever struggling prey may be captured within the mouth cavity. The prehension of food by the eyeballs is a unique adaptation not generally employed in the animal kingdom!

Included among the derivatives of the myotomes of the head, in all vertebrates except fishes, are the muscles supplied by the XIIth cranial nerve

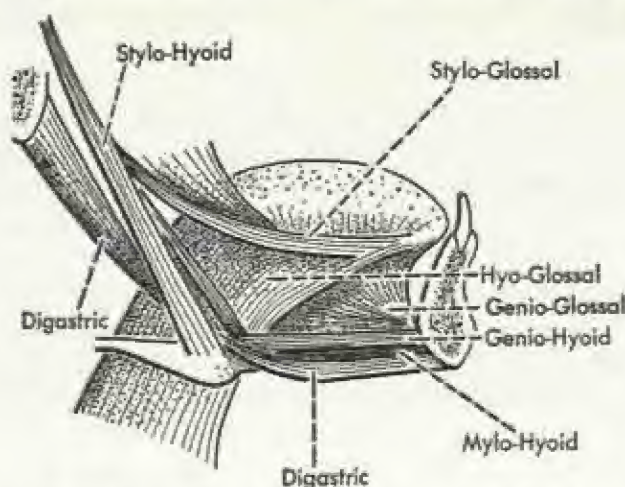


Fig. 585. Extrinsic muscles of the human tongue. (After Gegenbaur.)

(hypoglossal). This nerve, with its muscle segments that have to do with the tongue (Fig. 585) probably represents the fusion of several neuro-muscular units that have been incorporated into the head region from the metameric vertebral series at the anterior end of the spine. In most vertebrates these muscles, namely, the *hyoglossal*, *styloglossal*, and *geniohyal*, are extrinsic, that is, not forming a part of the tongue itself, but in mammals an additional muscle, the intrinsic *lingualis*, makes up the bulk of the fleshy tongue.

(b) **Trunk.**—In amphioxus and cyclostomes, without a definite lateral line, the muscles of the trunk and tail are undifferentiated, but in fishes they are divided as a rule by the horizontal skeletogenous system into the *epaxial* and *hypaxial* regions which are supplied respectively by the dorsal and ventral rami of the spinal nerves. These two general muscular regions undergo different fates in the course of further evolution and development.

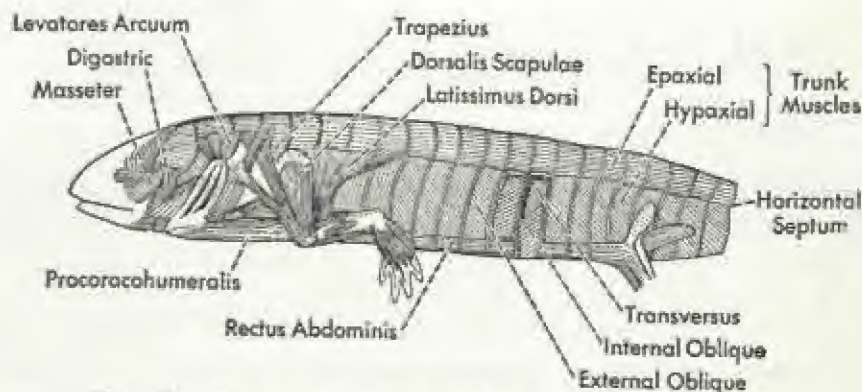


Fig. 586. The musculature of a salamander. (After Bütschli.)

The *ventral trunk musculature* of urodeles becomes delaminated into four sheets of muscle with the gradual obliteration of the myocommata that separate the myotomes from each other. Along the midventral lines on both sides of the linea alba, the muscle fibers still retain their original longitudinal arrangement, together forming a flat band of muscle, the *rectus abdominis*. Laterally, however, the body wall is composed of three layers, with the fibers of each layer assuming different directions. Next to the peritoneum the innermost layer, or *transversus abdominis* muscle, has fibers tending to run around the body at right angles to the long axis. Outside the transversus are two diagonal layers, the *internal* and *external oblique* muscles, having fibers at right angles to each other (Fig. 586).

In reptiles such as lizards and alligators, the ventral axial muscles are still further modified in the anterior half of the trunk region by the intro-

duction of encircling ribs. Posteriorly in the belly region the original three layers of muscles remain unchanged, but anteriorly in the thoracic region the oblique muscles become broken up into *external* and *internal intercostal muscles*, which extend from rib to rib and aid in respiratory movements. In the neck region in front of the ribs the oblique layers furnish material for the *scalenus muscles*.

Among birds the oblique muscles are poorly developed, the transversus is absent, and the rectus abdominis, reduced in size, is posteriorly unsegmented. This sacrifice of the ventral axial muscles is compensated, however, by an excessive elaboration of the appendicular muscles of flight, which come to overlie the muscles of the body wall. A familiar example of them is the "white meat" on the breast of roast chicken.

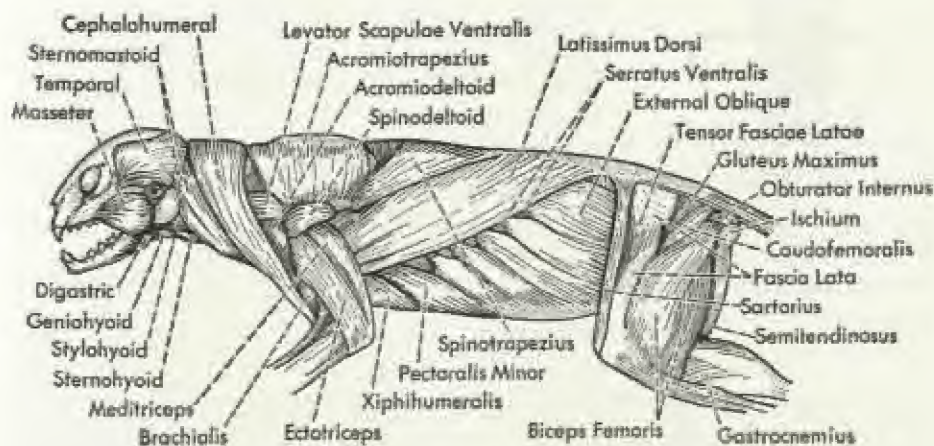


Fig. 587. The muscles of a cat. (After Sayles.)

The oblique muscles in mammals give rise to the *intercostal* and *serratus muscles*, which come to assume more of a dorsal than ventral position, although still supplied from the ventral branch of the spinal nerves (Fig. 587). Other mammalian muscles of ventral axial origin are the *psoas muscles* of the posterior abdominal wall, and the *colli muscles* of the neck region.

Furthermore, even in the reptiles the rectus abdominis muscle loses its primitive character by the introduction of the neosternum, so that it is broken up into presternal and poststernal parts. Some of the presternal muscles are the *sternohyoid*, *sternothyroid*, and *thyrohyoid* of the neck region. The poststernal musculature retains somewhat more of its primitive character, even up as far as the mammals, where traces of the myocommata

in the form of the *inscriptiones tendineae* may still be seen through the skin as depressions of transverse connective tissue interrupting the broad flat abdominis muscle. These depressions are represented by sculptors of classical times on the abdomens of many Greek heroes, a curious incidental evidence of the retention of these telltale ancestral marks in man until comparatively recent times (Fig. 588).

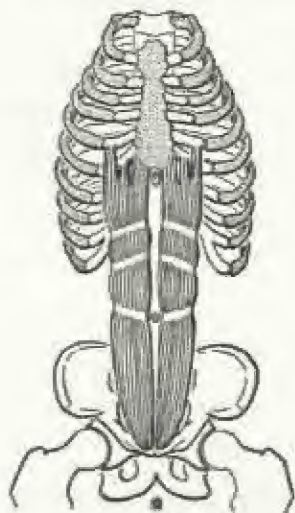


Fig. 588. The rectus abdominis muscles in man, showing the transverse *inscriptiones tendineae*. (After Mollier.)

The myotomes of the tail region are of great importance to fishes, enabling them to swim. Although little modified these primitive myotomes function adequately because the lateral movements of the tail are not complicated. In higher forms the caudal myotomes lose their original significance, and become reduced into muscles modified sufficiently to control the varied tail movements of such land animals as support a caudal appendage. Others become entirely freed from skeletal connection in the anal region and are transformed into *sphincter muscles*.

The *dorsal axial musculature* differentiated more slowly, but eventually, with the development of vertebral processes offering places of attachment, it gives rise to a greater array of separate muscles than is found below the

lateral line. In the consideration of these dorsal axial muscles care must be taken to avoid confusion with the appendicular muscles with which they are intimately involved.

Fishes and urodeles show little differentiation of dorsal-axial musculature, but reptiles have gone far enough in the elaboration of the neural arches of the vertebral column and its processes to give foothold to a large number of small muscles that, with their tendons and ligaments, tie together the different vertebrae.

The largest dorsal muscle is the *longissimus dorsi*, which extends lengthwise between the neural spines and the transverse processes. Groups of shorter muscles, metamerically arranged, extend (1) from one transverse process to another, *intertransversales*; (2) from the neural spine of one vertebra to the transverse process of the one in front of it, *transversospinales*; (3) from the transverse process to the ribs, *transversocostales*; and (4) from one spine to another, *interspinales*.

In birds the dorsal muscles of the rigid thoracic area are largely atro-

phied, except in the neck region where they are very much elaborated, as may be readily seen in the neck of a roast chicken.

The dorsal axial muscles of mammals resemble those of reptiles rather than those of birds, but are influenced more than in either of these groups by the appendicular musculature which increases much in importance.

(c) **Diaphragm.**—The lung-filling *diaphragm*, ordinarily unseen and unsung but described by one appreciative biologist as the indispensable "creator of all human acts," is an organ that plays a necessary part in the release of energy in every mammal.

It is a dome-shaped muscular structure coming from the ventral axial elements in the neck region and assuming, after gradual displacement and growth, a transverse position across the bottom of the thoracic basket (Fig. 336). It is pierced by the esophagus and by large arterial, venous, and lymphatic trunks, as well as by the tenth pair of cranial nerves (*vagus*), and the sympathetic trunk. Its own supply, as already stated, comes from the cervical region in the form of the *phrenic nerve*.

The non-muscular *transverse septum*, which partitions off the pericardial cavity from the body cavity in lower vertebrates, probably contributes to the median ventral quarter of the muscular diaphragm of mammals.

(2) **APPENDICULAR MUSCLES.**—Muscles of the appendages are derived from myotomes of the axial musculature. In the case of elasmobranch fishes, for example, at the region where the pectoral and pelvic fins are to become established, the ventral ends of the lateral myotomes sprout out *myotome buds*, two for each myotome (Fig. 526), which later become the *fin muscles*. Not only do the myotomes which are exactly opposite the future fin produce these buds, but several others immediately anterior and posterior to them also crowd together, adding contributions. As a result a generous number of muscular elements takes part in the formation of the fin musculature, the accompanying augmented nerve supply being sufficient to form a plexus of nerves which adequately insures effective performance of the fins.

Most of the appendicular muscles of mammals are considered to be primarily of myotome origin despite the fact that during embryonic development they arise, not from myotomic buds as in fishes, but from mesenchyme cells which migrate into the limb-buds.

In general the locomotor muscles may be classified into two groups, extrinsic and intrinsic, although the distinction is not always unmistakable.

(a) **Extrinsic Muscles.**—*Extrinsic muscles* serve the girdles and the proximal ends of the appendages. They connect the appendages with the

axial skeleton and move the limbs as a whole. *Intrinsic muscles*, on the other hand, have both origin and insertion within the appendages, effecting movements only in parts of them.

Among fishes the extrinsic group is most in evidence, consisting of *elevators* and *depressors*, which lift and lower, and *abductors* and *adductors*, which extend the fins and hug them next the body respectively. All of these muscles move the fin *as a unit*, and since there is little occasion, in the performance of mass movements useful in a water medium, for the niceties of movement effected by intrinsic muscles, these are absent.

The extrinsic muscles of the pectoral appendages are better developed than those of the pelvic appendages, owing to the difference in attachment of the respective girdles to the axial skeleton. The girdle of the pelvic appendages is anchored securely to the backbone, and so they require fewer intermediary muscles than the pectoral appendages, which are often entirely unattached by direct skeletal elements. In the pectoral appendages, particularly of birds, the extrinsic muscles reach a high degree of development, being packed for the most part on either side of the keeled sternum, and quite covering over and obscuring the axial muscles. The muscles of flight in a pigeon, for example, may equal as much as one fifth of the entire body weight.

(b) **Intrinsic Muscles.**—The *intrinsic muscles* of the appendages, which increase in number with the establishment of systems of appendicular levers in connection with land life, include *pronators*, *supinators*, and other rotators as well as *extensors* and *flexors* of the forearm, shank, hand, foot, and digits. In primates, including man, these muscles are more primitive than in many other vertebrates. This is because the generalized pentadactyl skeletal framework is still retained in primates, while in many other vertebrates there is a reduction of distal skeletal parts and a consequent modification of the musculature. The generalized pentadactyl appendages of man are among the factors contributing largely to his dominance. More possible avenues of diversified activity are by this means left open than when extreme specialization takes place, as in the flipper of a whale, the wing of a bird, or the leg of a horse.

2. Branchiomic Muscles

The muscles of the splanchnocranium are derived from the ventral hypomeric part of the mesoderm which remains after the myotomes have become established. They are associated with the skeletal parts representing a "boom that failed," in the evolutionary sense. Consequently they undergo many makeshifts with the modification or disappearance of their original

skeletal connections. These muscles of the splanchnocranium, although visceral in origin, are striated and voluntary in action.

The branchiomeric musculature is most evident in elasmobranch fishes, where four groups according to nerve supply may be clearly distinguished, namely, the trigeminal, facial, glossopharyngeal, and vagus. Despite all of the changes in the branchial arches from elasmobranchs to mammals the same four groups of muscles are retained in higher forms.

To the *trigeminal-nerve* (V), or *mandibular-arch*, group belong such muscles of mastication as the *temporalis* and *masseter*, which raise the lower jaw, and the anterior belly of the *digastric*, which depresses this structure. In man the masseter, which runs from the lower edge of the malar bone to the outside of the lower jaw, may be easily demonstrated by placing the finger tips upon the cheeks in front of the ears and biting the teeth together. In the same way the temporalis may be located by pressing upon the temples and biting. Another member of this group in mammals is a tiny middle-ear muscle, the *tensor tympani*, with its insertion on the malleus, a derivative of the embryonic mandibular arch, as we have seen in Chapter XVII.

The *facial-nerve* (VII), or *hyoid-arch*, group includes the *stylohyoid*, extending between two parts derived from the embryonic hyoid arch, and the posterior belly of the *digastric*, as well as the muscles of facial expression described in the section on integumentary muscles which follows. The *stapedius*, which is inserted on the stapes, a derivative of the embryonic hyomandibular, is probably the smallest striated muscle in the vertebrate body.

The *glossopharyngeal-nerve* (IX) group, associated with the first-functional-gill arch of elasmobranchs, contributes to the pharyngeal musculature of mammals.

The *vagus-nerve* (X) group includes the muscles which spread open and close the last four gill arches in respiration in elasmobranchs, and so long as they remain in other groups. In higher forms, when the *spinal accessory nerve* (XI) becomes admitted to the fraternity of cranial nerves, it joins with the vagus. In mammals these two nerves together innervate most of the pharyngeal muscles as well as those of the larynx. In addition they supply two muscles connected with the pectoral girdle, the *trapezius* and the *sternocleidomastoid*.

3. Integumental Muscles

The *integumental*, or *dermal*, muscles split off embryonically from the underlying skeletal muscles. While in many cases retaining their skeletal

origins at one end and inserting under the skin at the other, they sometimes, as in sphincter muscles, lose all skeletal connection.

The tight-skinned fishes are without any dermal musculature, and amphibians have only a trace of anything of the sort in the tiny muscles that open and close the lids of the nostrils.

Snakes among reptiles use integumental muscles in locomotion, for these muscles enable the scales to get a grip on the ground. This fact can be easily demonstrated by placing an active snake upon a level surface of glass and observing the difficulty it encounters when the dermal muscles are thus made ineffective on a surface that cannot be gripped by scales.

Birds fluff the feathers by means of integumental muscles, in this way changing the thickness of the layer of warm air held next the body to regulate the body temperature. The so-called *patagial muscles* in the web of a bird's wing, that assist in flight, belong to the integumental group and are derived from the pectoralis muscles of the breast, together with various muscles of the shoulder and arm.

It is in mammals, however, that integumental muscles reach their greatest differentiation, serving a wide range of uses from defence to the expression of the emotions.



Fig. 589. European hedgehog, *Erinaceus*, with the skin removed, showing the manner in which it rolls up by contraction of the integumental musculature. (After Nuhn.)

Under *defensive skin muscles* may be mentioned (1) those which cause hairs and bristles to stand on end in terrifying fashion, as on the tail of a frightened cat or on the scruff of an angry dog's neck; (2) those which erect defensive spines or quills, as in the skin of the "fretful porcupine," *Erethizon*; (3) those which enable animals like the armadillos and the European hedgehog *Erinaceus* (Fig. 589), to roll up into an impregnable ball; and (4) muscles which tend to dislodge annoying insects by causing the skin to shudder or twitch, as on the neck, shoulders, and the anterior

sides of a horse, but which are less evident or necessary on the hips and flanks within reach of the swishing tail (Fig. 590).

Integumental muscles play a leading rôle in the *expression of the emotions*, particularly in man. This phase of biology has been elaborated into a subsience by Lavater (1741-1801) and his disciples under the name of *Physiognomy*. Charles Darwin had something to say on this theme in his book entitled *The Expression of the Emotions in Man and Animals*.

Generally speaking there is no great expression of the emotions by means of facial muscles in the lower animals. The "state of the mind," whether it be fear, anger, or excitement from any cause whatsoever, is usually shown by movements and attitudes assumed by the body, rather than by the action of the skin muscles of the face. Most animals may be said to have a "poker face," which does not reveal what may be mentally happening behind the facial mask. Whatever expression shows is usually centered in the eyes. In the rigid face of a fowl, for instance, the lively eye gleams like a jewel.

Among carnivorous animals and primates the dermal muscles of the face take on character, until in man it is the evanescent expression wrought by facial, or "mimetic," muscles, so difficult to analyze and to image by the artist, that remains in the memory long after the form of the body is forgotten.

The facial muscles that are most expressive in man and least developed in brutes are those located at the inner extremities of the eyebrows and at the angles of the mouth.

Voluntary integumental muscles fall into two general groups according to their derivation: first, the *panniculus carnosus* group from the latissimus dorsi and pectoralis muscles, and second, the *sphincter colli* group, from the branchiomeric musculature of the hyoid region, under the dominance of the seventh pair of cranial nerves.

The *panniculus carnosus* is particularly evident in mammals, although somewhat degenerate in man, and with only primitive traces showing in the lower vertebrates. It is a thin sheetlike muscle that tends to wrap about the body under the skin. In monotremes it extends over the entire body as far



Fig. 590. The integumental muscles of a horse, by means of which the skin may be "shuddered" for dislodging annoying insects. These muscles are absent on the flanks, which can be reached by the swishing tail. (After Nuhn.)

as the cloaca, and includes a *sphincter marsupii*, and a *sphincter cloacae*. In the porqual, *Balaenoptera*, it likewise extends from the mouth to the anus, while in the "right whale," *Balaena*, it is restricted to the head region.

Fragments of the enveloping panniculus carnosus remain longest in the axillary, inguinal, and sternal regions. These fragments make up the shuddering muscles of the horse, already referred to, and the muscles by which a wet dog shakes itself. There is also occasionally a *sternalis* muscle under the skin and superficial to the pectoralis, which is sometimes visible in man when well enough developed.

The progressive *sphincter colli* group of integumentary muscles, originally associated with the hyoid arch, is supplied by the facial (VII) nerve. In such animals as turtles and birds it is a well-developed group of muscles enwrapping the neck. During its evolution it migrated forward and expanded so as to spread over the head and down onto the shoulders, becoming differentiated into a superficial sheet of muscle designated as the *platysma* and the deeper lying *sphincter colli proper*.

With the upgrowth of the cranium that part of the *platysma* extending over it becomes divided into an occipital and a facial part, separated by a broad sheet of connective tissue, the *galea aponeurotica*, that stretches over the top of the cranium under the skin. The facial parts of the *platysma* and *sphincter colli* may be classified into four groups of muscles in close association with the underlying muscles of mastication. These are the muscles of the external ears, eyebrows, nostrils, and lips and cheeks (Fig. 591).

The muscles of the external ear, namely, *auricularis anterior*, *posterior*, and *superior*, enable an animal to turn the pinna of the external ear toward the source of sound without changing the position of the head. They are better developed in animals like dogs and horses than in man, although fragments still remain enabling some individuals to entertain their friends by wiggling their ears.

The eyebrow group takes in four muscles: the *frontalis*; *orbicularis oculi*; *levator palpebrae superioris*; and *corrugator supercilii* or brow-wrinkler. The eyebrow has been poetically described as "the rainbow of peace and the bended bow of discord."

Three more or less well-developed muscles of the nostril group are the *levator labii superioris et alae nasi*, by means of which man as well as beast sneers and snarls; the *dilatatores naris* and the *compressor naris*, by means of which rabbits and men wiggle their noses.

Finally, the lips and cheeks group consists of a strong sphincter muscle, the *orbicularis oris* around the mouth opening, from which radiate several other muscles. Of these the *risorius muscle*, attached at the corners of the

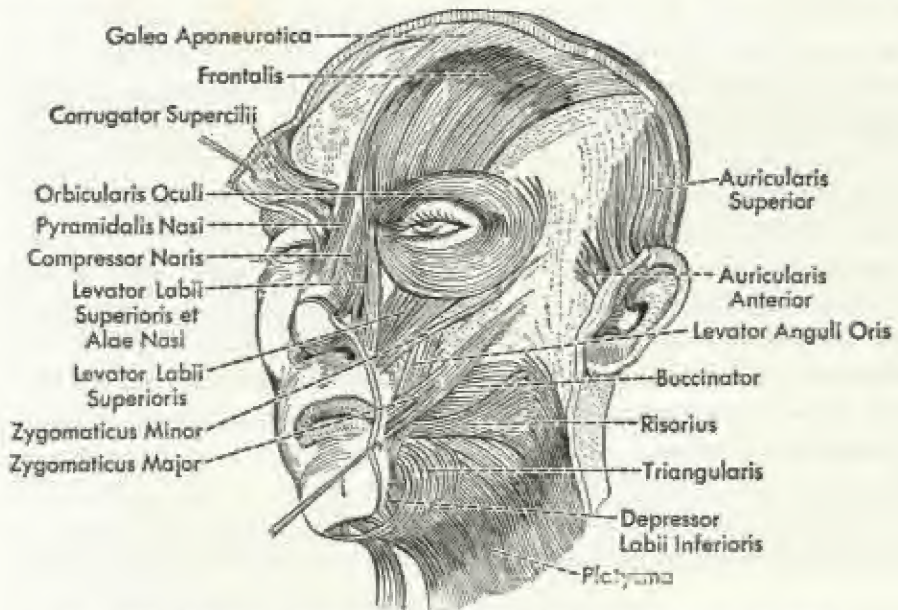


Fig. 591. Mimetic muscles (muscles of facial expression) in man. (After Toldt.)

mouth opening and pulling laterally in opposite directions, and the *triangularis*, pulling down the corners of the mouth, serve in humankind to express the diverse emotions of laughter and tears. The *buccinator* makes up much of the cheek wall.

The facial muscles of expression of the ear group may be regarded as *regressive* or degenerate, so far as man is concerned, having disappeared entirely in a considerable percentage of individuals, while the "psychological muscles" of the face that accompany increasing intelligence and reach their highest differentiation in man, are *progressive* muscles, the evolution of which is by no means yet completed.

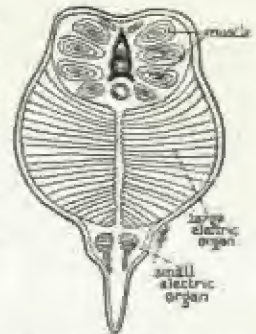


Fig. 592. Electric organs of an electric eel, *Gymnotus*. (After Haller.)

VII. ELECTRIC ORGANS IN FISHES

In a few exceptional instances among elasmobranchs and teleosts, for example, the electric ray *Torpedo*; the electric eels, *Electrophorus* and *Gymnotus* (Fig. 592); the star-gazer *Astroscopus*; and the African *Malapterurus*, certain muscles have become transformed into electric organs, which

in the emergency of an attack can deliver a shock, more or less effective, to other animals. The voltage of the discharge by adult specimens of *Electrophorus* has been found to average 370 volts but one case has been reported of a maximum discharge of 550 volts.

Structurally these electric organs consist of a number of regularly arranged elements, called *electroplaxes*, put together in histological layers that resemble alternating plates in a storage battery. It is not difficult to imagine how these structures have developed from muscles, since normally muscles in action discharge a certain amount of electricity. The fact that the mechanism, although developed in different parts of the body in different species, is always derived from muscular tissue, indicates that it is a physiological adaptation and not a morphological inheritance of one species from another.

The Dominating Factor—Nervous System

I. GENERAL CHARACTER

It is fortunate that the whole intricate nervous mechanism, consisting as it does of stimulus-receiving devices of various kinds, transmission cables and meshworks, and ganglionic masses with accessory supporting and protective parts, may be resolved into component units, both structural and functional, and thus may be rendered intelligible. The untangling of the nervous system constitutes one of the most intriguing chapters in the whole story of comparative anatomy.

This important and dominating mechanism is for the most part out of sight behind the scenes and apparently quite secondary to the skeletal framework, visceral parts, and musculature that determine the general contours of the body. Yet if by some magical technic the entire body substance except the ubiquitous nervous apparatus with all of its infinitesimal ramifications could be harmlessly spirited away, there would still remain in place a gauzy fabric of innumerable spidery cells and finespun fibers that would preserve completely in ghostlike form the original outlines of the body.

The nervous system is a conducting apparatus that receives sights, sounds, and other physical as well as chemical contacts in an ever-changing environment, and hands them on to centers of judgment and adjustment within the organism itself, which, in turn receiving aid from other conducting mechanisms, brings about action by means of arousing or restraining contractile or secretory tissues. Any physical or chemical change which excites (arouses to activity) a nerve cell is known as a *stimulus*. From the point of stimulation an *impulse*, or self-propagating change within the nerve cell, passes along the cell as the "message" carried by the "transmission line."

In higher animals such as man the nervous apparatus includes the seat of intelligence, the storehouse of memory, and the headquarters of the affections and the will. Even in so-called "lower" animals the beginnings of these desirable acquisitions appear.

The great importance of the nervous system is shown by the fact that it is laid down very early in embryonic development, outstripping all other groups of tissues during the first great onrush of embryonic growth. As Wiedersheim has pointed out, it presents comparatively few rudimentary or degenerate structures.

II. THE STRUCTURAL UNITS

As would naturally be expected, the *ectoderm*, that is, the embryonic tissue which presents primary contact with the environment, gives rise to the principal cell units destined to form the nervous system. These ectodermal cells eventually depart very far from their original epithelial compactness,

becoming either true nerve cells (*neurons*), or non-nervous structures (*neuroglia cells*), which have a secondary supportive rôle.

Still other cells, from the embryonic *mesoderm*, may also serve the all-important neurons in the form either of nutritive blood or as protective coverings.

The *neuron theory*, which is the most commonly accepted working hypothesis of biologists concerned with the nervous system, holds to two propositions: first, that the nervous system proper is entirely made up of neurons; and second, that transmission of nerve impulses from one neuron to another is by means of make-and-break contact without protoplasmic fusion.

The point of contact between neurons is called a *synapse*. The entire working nervous system in man involves several hundred million synapses.

After differentiation from their generalized spherical embryonic form, neurons come to vary enormously in size, shape, thickness, length, and manner of their insulation.

The cell body immediately surrounding the nucleus sprouts out into various *processes*, the so-called "*nerve fibers*," which may become enormously attenuated and lengthened (Fig. 593), although always remaining an essential part of the cell and under immediate control of the nucleus. Thus the neuron assumes a form well adapted to its primary function of transmission at the same time that it is specializing in sensitivity,

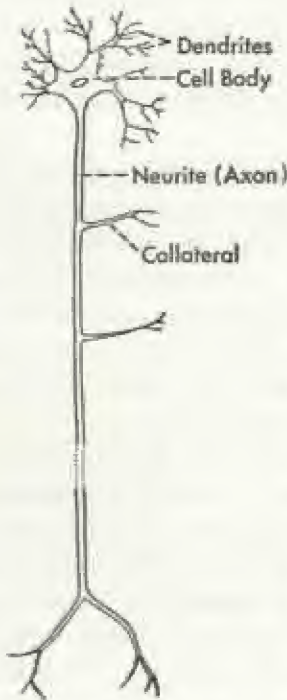


Fig. 593. A nerve cell.

a function which is simply one of the general endowments common to all cells.

By "joining hands" in synapses the long, drawn-out neurons form continuous living bridges and networks that connect points of stimulation with points of reaction. In short they are conductors which, like telegraph wires, permit the passage of messages while remaining stationary themselves.

The more recently developed *neurohumeral theory** points out that transmission from neuron to neuron, in some instances at least, may depend not upon direct contact, but be due to the hormonal production of "neuro-humors" that make a bridge at the junction of one neuron with another over which impulses may pass.

The extended fibers of certain nerve cells in man may reach an actual length of three feet from nerve cord to toe tip, an astonishing span for any single animal cell to attain. The end of such a fiber is thus frequently much nearer to the nucleus of some neighboring cell with which it may come into synaptic touch than with its own nucleus.

Until the *neuroblasts*, or embryonic neurons, have sprouted out their cell processes sufficiently to make contact possible, the transmission of impulses cannot be even temporarily established. These pathways are thus gradually set up and any break in the network of links interrupts the operation of the whole system to some degree. One explanation of unconsciousness and sleep is that for the time being the integrating synapses between some of the neurons are at least partially interrupted.

i. Polarity

The capacity for conduction through valvelike synapses results in *polarity*, or one-way traffic, within the individual neurons. Impulses enter along certain fibers or processes and depart by others, a relation which is never reversed. The fibers forming incurrent pathways, with respect to the nucleus and cell body, are known as *dendrites*, because they frequently present abundant treelike arborizations. The excurrent pathway, on the other hand, is through a single special fiber, called the *neurite* or *axon*, which is usually larger and much longer than the more numerous dendrites and not so much given to branching. Whenever branching does occur in a neurite, the twigs, or *collaterals*, except at the tip of the neurite, characteristically leave the main fiber at right angles instead of by acute angles as in the case of dendrites (Fig. 593).

* Parker, G. H., *Nervous Activity by Humors, with Special Reference to Chromatophores*, Cambridge University Press, 1932.

Neurons may be *bipolar* or *multipolar*, according to the number of fibers present. The more primitive bipolar type, with one centripetal dendrite and one centrifugal neurite, is found in fishes, and also in the dorsal ganglia of

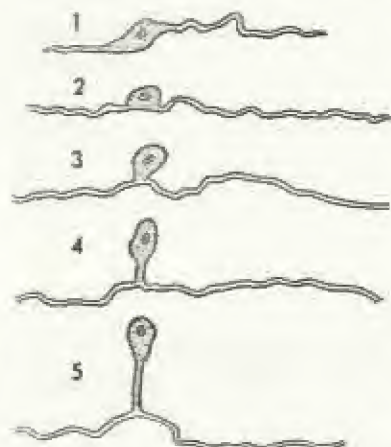


Fig. 594. Stages in the transformation of a bipolar neuron into an apparently unipolar one.

higher vertebrates. Multipolar neurons, on the other hand, have several dendrites and a single neurite. The apparently unipolar type in dorsal ganglia, results when the proximal ends of a dendrite and a neurite appear to emerge together from the cell body. In reality, however, they are brought around side by side as a result of the mechanics of growth and are quite independent morphologically from each other, although taking on secondarily a unipolar appearance (Fig. 594).

When a neurite ends in a muscle fiber or a gland, it may enlarge into a flattened *end plate* or *bulb*, or expand into a tiny *brush*, or end simply like a *thread*. The distal tips of neurites and dendrites, at the points of synapsis, form the weakest links in the chain of neuronic elements.

2. Nerve Fibers and Their Sheaths

Nerve fibers fall into four categories with respect to the degree and manner of sheathing, as follows:

- (1) Naked fibers without sheaths, occurring in the "gray substance" of the central nervous system.
- (2) Fibers with a protective *neurolemma*, or *Schwann's sheath*, characteristic of invertebrate "nerves" generally; in the nerves of amphioxus and the cyclostomes as well as the olfactory nerves of other vertebrates; and at the distal ends of the spinal nerves. Fibers of this type are known as *Remak's fibers*.
- (3) Fibers with an insulating sheath of fatty or lipid substance, the *medullary*, or *myelin, sheath*, occurring in the "white substance" of the central nervous system.
- (4) Fibers with both sheaths present, the medullary sheath within Schwann's sheath. This type occurs in nerves generally, except at the ends.

The neurolemma, composed of ectodermal cells derived from the original medullary tube, is a very thin, living sheath while the myelin sheath is a thicker, secreted layer which is white in color in fresh tissue. Probably the neurolemma secretes the myelin material, but only in the presence of the nerve fiber. Nervous tissue in which *myelinated fibers* predominate is white in color while cell-bodies and *unmyelinated fibers*, either naked or Remak's fibers, being composed of living protoplasm, form "gray matter."

In the case of fibers covered by both sheaths, the medullary sheath, but not the neurolemma, is interrupted at frequent intervals along the fiber, at the *nodes of Ranvier* (Fig. 595). Each internodal ("between the nodes") region is associated with a single neurolemma cell containing a conspicuous nucleus. When the myelin sheath alone is present it is not segmented but forms instead a continuous tubular covering over the fiber.

All these types of fibers and their sheaths are diagrammatically represented in Figure 595.

3. Microscopic Structure

Microscopic examination of a neuron after proper staining reveals structural details of great complexity.

Neurofibrils, like myofibrils in a muscle cell, extend through the cell from end to end. They also surround the nucleus. In all probability they are highly elaborated parts of the cytoplasm directly concerned with the transmission of nerve impulses. Around the nucleus and in the dendrites, but not in the neurite, is found the so-called *tigroid substance*, or *Nissl bodies*, which apparently plays some part in the metabolism of the neuron, since it varies in amount in accordance with the amount of work done.

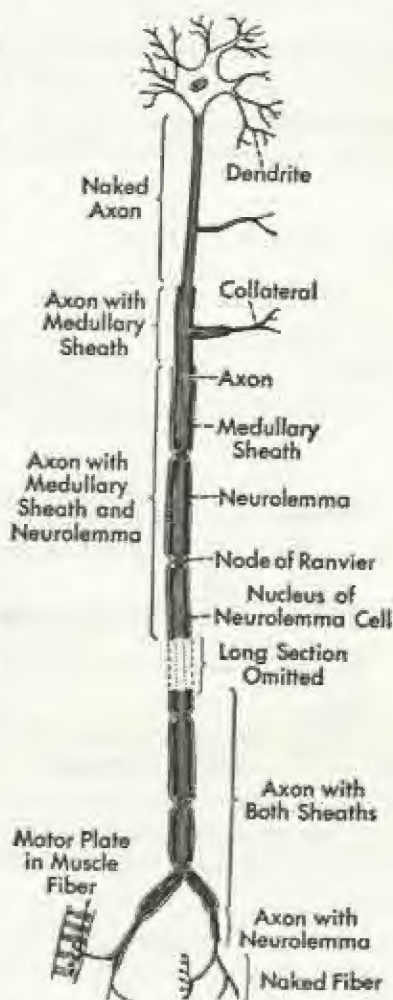


Fig. 595. Diagram of a multipolar neuron with sheaths.

Another cytoplasmic structure of problematic function, which is particularly characteristic of neurons, is the *Golgi apparatus*, an anastomosing network near the nucleus. In spite of the triumphs of histological discovery, much still remains to be found out. Our present knowledge of the marvelous units of the nervous system might be compared to what it would be possible to learn of short wave transmission by examining the picture of a cross section through a house that has a radio in it. With increasingly refined technic what new discoveries has the neurologist of the future in store!

III. REFLEX ARCS

The functional units of the nervous system as contrasted with the structural units are called *reflex arcs*, which involve two or more neurons, and in addition a non-nervous element in the form of a muscle cell, for example, or a gland cell that acts in consequence of the stimulus received.

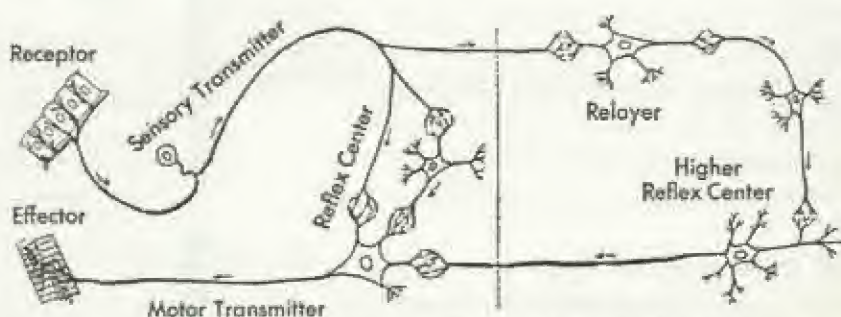


Fig. 596. The plan of a reflex arc. To the left of the dotted line are shown simple two- or three-neuron reflexes; the entire diagram shows a more complex reflex involving more neurons.

A reflex arc consists in each case of at least five fundamental links, each with a different function, namely: (1) a *receptor*; (2) a *sensory transmitter*; (3) a *reflex center*, including the synapse; (4) a *motor transmitter*; and (5) an *effector* (Fig. 596). Together these five links form a living chain or bridge extending from the point of stimulation to the organ which functions as an effector. The receptor and the sensory transmitter together consist of a single neuron, so placed as to receive stimuli at the dendritic pole of the cell body, either from the outside world or from within the body itself, while the neurite, or axon, becomes the sensory transmitter to another neuron.

Centers, in which synapses determine the courses to be taken by impulses

and consequently what is to be done, are usually withdrawn from the surface into a region protected from the direct bombardment of stimuli. A neurite extending from a cell body in the center forms the motor transmitter, or the fourth link in the chain that carries the decision of the center to the effector (Fig. 597).

The most numerous effectors in reflex arcs are no doubt muscle cells, although glands, luminescent organs, and chromatophores, which are modifiable pigment-bearing cells, are also effectors that respond to stimuli by action of some sort.

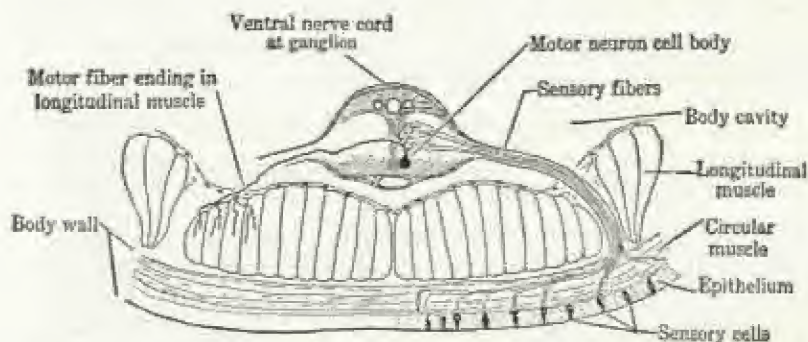


Fig. 597. Cross section of the ventral nerve cord and surrounding structures of an earthworm. (From Woodruff, *Animal Biology*, copyright 1941, by permission of The Macmillan Company, publishers.)

Of the two fundamental neurons in a reflex arc the sensory cells usually have long dendrites and short neurites, while the reverse is true of motor cells. Such simple reflexes, involving only two neurons, are extremely rare. Possibly the knee-jerk is one. In most reflex arcs one or more additional, intermediate links, the so-called *association neurons*, or *relayers*, are inserted between the sensory and the motor neurons. A large part of both the spinal cord and the brain is made up of such intermediate neurons which increase the distance in the chain between receptors and effectors, making complex relationships not only possible but inevitable.

An association neuron not only lengthens its special line of communication, but also makes possible a hook-up with other lines. Thus single effectors may receive impulses from several receptors at the surface or impulses starting at a single receptor may go to several different effectors at once. In either case the receptor, relayer, and effector make a trinity that acts as a unit.

IV. PRIMITIVE NERVOUS SYSTEMS

It took a long time to develop the complex human nervous system. In a simple animal like an *Amoeba*, the whole body is a single cell-mass of protoplasm, possessing a generalized capacity for irritability and contractility. Whenever a stimulus impinges at some spot on such a body there results a direct local response at the point of stimulation, but the news of it travels slowly to other parts of the cell. The fact that an *Amoeba* in escaping from danger extrudes a pseudopod on the side opposite to the point of stimulation is an indication that some degree of protoplasmic conduction is present even here. It is out of the question in such a case to speak of sense organs or receptors, of communicating nerve fibers, adjusting centers or of reacting muscles, because they have not yet developed.

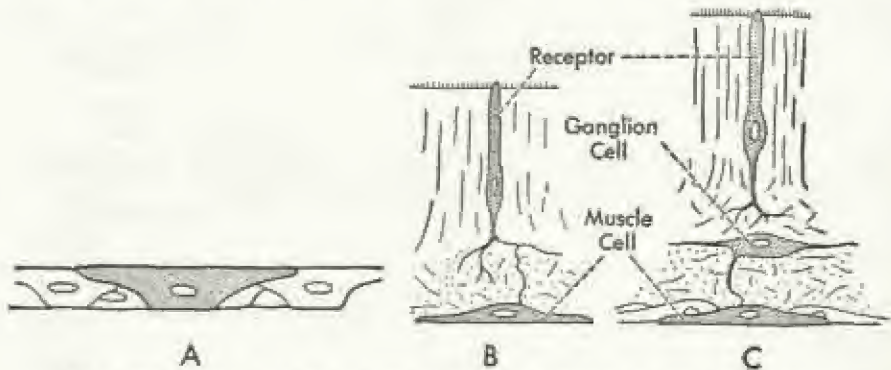


Fig. 598. Diagrams of primitive nervous systems. A, an independent effector, a muscle cell such as occurs in the most primitive multicellular animals; B, simple receptor-effector system as found in tentacles of sea-anemones; C, more complex type of receptor-effector system, with the insertion of a so-called ganglion cell, as seen in various parts of the sea-anemone. (After Parker.)

It has been suggested that the coelenterates show what may have been the first steps in the evolution of the neuromuscular mechanism. In *Hydra*, for example, the inner ends of some of the surface ectodermal cells develop muscular processes. When these cells are stimulated their inner portions contract without mediation of any sensory receptor. Parker has given the name *independent effector* to this type of cell which serves as both receptor and effector (Fig. 598).

In most animals, including many coelenterates, these two functions are performed by separate cells. In the simplest arrangement *sensory cells* (receptors), exposed to the outside, are in direct contact, through their

branching inner ends, with underlying contractile *muscle cells* (effectors). Usually, however, a second nerve cell, a *motor cell*, is inserted between the sensory and muscular elements. In coelenterates the motor cells unite into a continuous network, *nerve net*, in which impulses may pass freely in any direction and consequently spread through the net to give a diffuse response to a localized stimulation. Nerve networks are found on vertebrate blood vessels (Fig. 599).

Simple localized reflex arcs including two short neurons persist in the walls of the digestive tube of man. By means of large numbers of these arcs, located in the *plexus of Auerbach* and the *plexus of Meissner*, the peristaltic response to the stimulating presence of food is brought about without the intervention of the cord or brain.

The final step is taken by the flatworms in which the synapses between sensory and motor neurons as well as the cell bodies of the latter are located in nerve cords. Also nerve impulses are transmitted in only one direction. Similar simple reflex arcs, involving a central nervous system, are found in most invertebrates (Fig. 597) and in the vertebrates.



Fig. 599. Nerve network from a small blood vessel in the palate of a frog. [After Prentiss.]

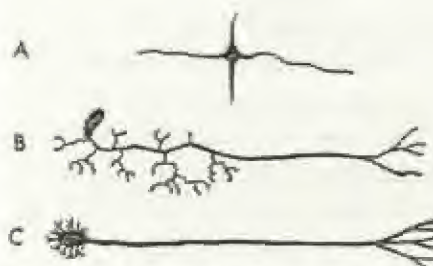


Fig. 600. Evolution of motor neurons. A, a protoneuron, from the nerve-net of a coelenterate; B, neuron from an earthworm; C, primary motor neuron of a vertebrate. In B and C the receptor end is at the left and the discharging end at the right. (After Parker.)

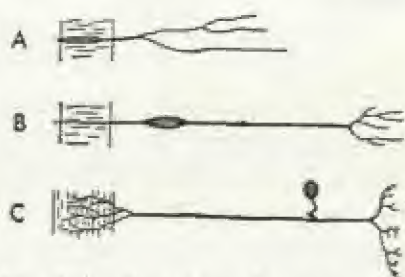


Fig. 601. Evolution of sensory neurons. A, from a coelenterate; B, from a mollusk; C, primary sensory neuron of a vertebrate. The cell body becomes more and more withdrawn from the surface. (After Parker.)

Primarily the cell bodies of sensory neurons are located in the surface epithelium, as we have seen in the coelenterates and worms. But frequently they shift deeper into the body and develop dendrites, which may be of considerable length if the cell body lies at some distance from the surface of the animal's body.

Steps in the evolution of motor and sensory neurons are shown in Figures 600 and 601.

V. THE EMBRYONIC RISE OF THE NERVOUS SYSTEM

In invertebrates generally the inward migration of the central nervous system comes about through a process of *delamination*, that is, the splitting off of a thickened band of cells from the hypodermis along the ventral side of the body (Fig. 4).

In the case of most vertebrates, on the contrary, the central nervous system is buried by a process of *invagination*. In cyclostomes and in many teleosts, however, the embryonic foundation of the central nervous system is probably laid down first as a solid rod of cells which afterwards becomes hollowed out.

The first step in the formation of the vertebrate nervous system occurs toward the end of the gastrula stage when the ectoderm in front of the blastoporic lip thickens to form the *neural* or *medullary plate*, which extends lengthwise along the dorsal side of the elongated embryo. This structure is morphologically continuous and, since the embryonic ectoderm is not conspicuously given to metameric expression, it is never marked off into segments, as in the underlying mesoderm in the formation of somites.

The lateral edges of the long flat medullary plate next become elevated, thus transforming it into a troughlike canal, the *medullary groove* (Fig. 113). Continuing their growth upward, the edges eventually meet and grow together, forming the *medullary tube*. The cavity within this embryonic tube is the forerunner of the *ventricles* of the brain and the *central canal* of the spinal cord. The closure of the tube begins in the middle region and extends both ways, so that for a time both ends still remain open.

At the posterior end there may exist, in addition to the trough-like opening to the outside, a temporary inward passage-way around into the primitive enteric cavity through the blastopore (Fig. 114). This is the *neurenteric canal*, which remains open up to the fourth week in the human fetus, although the medullary groove begins to close about the fifteenth day. The anterior end of the medullary tube remains unclosed longer than the posterior end in the form of the so-called *neuropore*. Amphioxus retains the neuropore throughout life. Possibly in this forerunner of the vertebrates it may serve as some sort of a sense organ.

As the medullary tube closes there form on either side along the seam of fusion two distinct ridges of medullary tissue, the *neural crests* (Figs. 602 and 603). At first continuous with the tube, these crests later gain independence by the insertion of invading mesenchymal tissue between them and the tube itself. Eventually the crests break up into chains, forming both

the sensory *dorsal ganglia* of the spinal nerves and the ganglia of the autonomic system, which are of motor function. When the neurons of the dorsal ganglia sprout they send their dendrites into the various organs of the body while their neurites establish a secondary connection into the cord. The autonomic ganglia also becomes connected with the cord, but by neurites which grow out from cells within the cord itself. Similar relationships are established in the brain region.

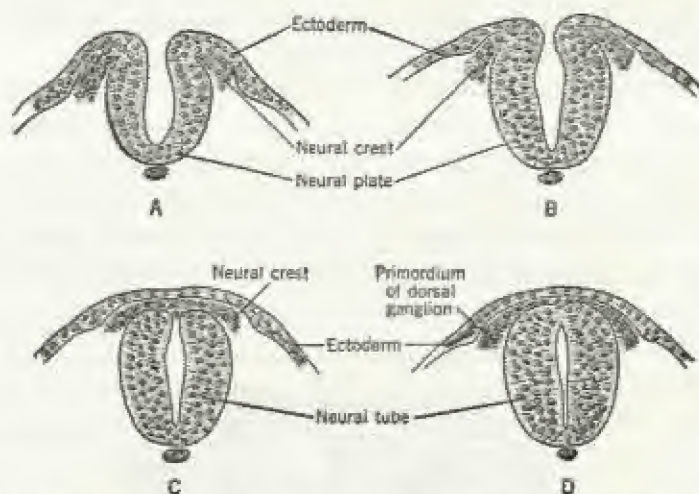


Fig. 602. Four steps in the formation of the neural crests during the closure of the neural tube in the pig. (From Messer, *An Introduction to Vertebrate Anatomy*, copyright 1947, by permission of The Macmillan Company, publishers. After Patten.)

All of the nervous tissues of the body are derived, either directly or indirectly, from the medullary tube, with the exception of cells and fibers that contribute to the olfactory epithelium.

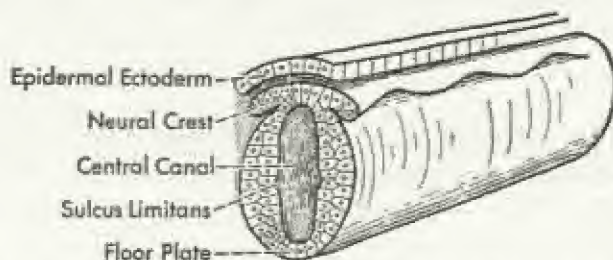


Fig. 603. Stereogram of early spinal cord, showing formation of neural crest. (After Kingsley.)

VI. SUBDIVISIONS OF THE NERVOUS SYSTEM

The vertebrate nervous system consists of three subdivisions, all intimately associated with one another, namely: (1) the *Central Nervous System*, consisting of the brain and spinal cord; (2) the *Peripheral Nervous System*, including the cranial and spinal nerves; and (3) the *Autonomic Nervous System* which is a special portion of the peripheral nervous system innervating smooth muscles and glands. *Sense Organs*, to be considered in Chapter XX, are made up of specialized endings of cranial and spinal nerves together with various non-nervous elements.

The peripheral nervous system is an indispensable auxiliary of the central nervous system. It consists of *nerves* and *ganglia*. Nerves are groups of fibers which put sense organs and effectors into physiological connection with the brain and cord, while ganglia are groups of cell bodies. Corresponding parts within the central nervous system are *tracts* and *centers*, respectively. In general the cell bodies of all sensory neurons are in ganglia while those of all motor neurons, except certain autonomic ones, are within the central nervous system.

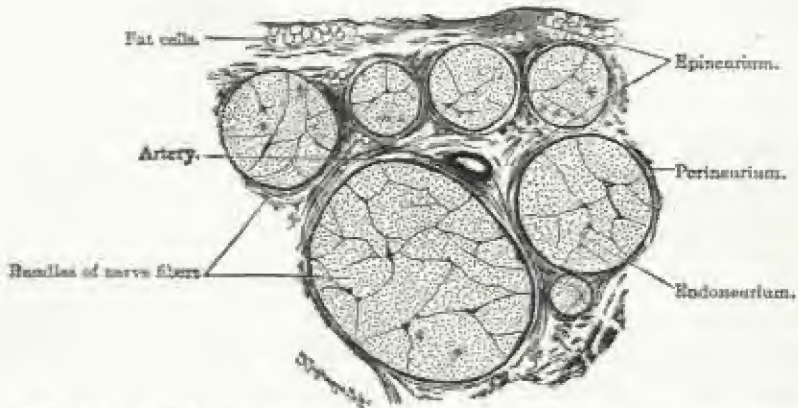


Fig. 604. Medullated nerve. Part of a cross section of a human median nerve. (From Bremer and Weatherford, *Lewis and Stöhr's Histology*, copyright 1944, by permission of P. Blakiston's Son and Company, publishers.)

"Nerves" are cables of neurites and dendrites in which the independence of the strands composing them is maintained. They extend through mesenchymatous tissues to all parts of the body, except into cartilage and the epidermal layers of the skin. Although the number of nerves is not large primarily, the neurons, or morphological elements that combine to make them (Fig. 604), may be, according to Donaldson, as many as three or four

millions in man. The nerves associated with the central nervous system are in pairs, and are either *spinal* or *cranial*, according to whether they connect with the cord or brain.

VII. THE CORD AND SPINAL NERVES

The cord and spinal nerves are so intimately related that it is difficult to obtain a clear understanding of the one without some knowledge of the other. They will therefore be considered together.

1. Form of the Cord

The human nerve cord may be used as the basis for the description of the cord, not only because it is of more immediate interest than that of other vertebrates, but also because much more is known about it.

With its ensheathing envelopes removed it is seen to be a slightly flattened tube, having a shallow median furrow running down its dorsal length (Fig. 605), and another wider and deeper groove along the middle of the ventral side. Other less conspicuous longitudinal furrows are also present, giving the whole cord somewhat the appearance of a fluted column.

At the anterior end where the cord passes over continuously into the brain, it appears broadened and somewhat oval in cross section, but at the posterior end it tapers rapidly and finally terminates in a non-nervous threadlike prolongation, the *filum terminale*, into which in early fetal stages the central canal of the cord still extends.

In two regions, at the level of the arms and the legs, the cord becomes swollen to an increased size. That these enlargements are associated with the increased nerve supply of the paired appendages is indicated by the fact that they are absent during embryonic growth before the limbs develop. In flying bats, as would be expected, the anterior far exceeds the posterior enlargement in size, while in leaping kangaroos, which have rudimentary dangling fore legs and powerful hind legs, the reverse is true.

Certain gigantic dinosaurs of the remote past, that were propped up upon a colossal underpinning of pillar-like legs, for example *Stegosaurus* (Fig. 36b), actually had a considerably greater diameter in the sacral region of the cord than in the brain itself,



Fig. 605. Diagram of the human cord, dorsal view, showing enlargements and *filum terminale*.

which inspired the famous columnist "BLT" of the *Chicago Tribune* to write:

"Behold the mighty dinosaur
Famous in prehistoric lore
Not only for his power and strength
But for his intellectual length.
You will observe by these remains
The creature had two sets of brains—
One in his head (the usual place),
The other at his spinal base,
Thus he could reason *a priori*
As well as *a posteriori*.
No problem bothered him a bit.
He made both head and tail of it.
If something slipt his forward mind
'Twas rescued by the one behind.
And if in error he was caught
He had a saving afterthought.
Thus he could think without congestion
Upon both sides of every question.
Oh, gaze upon this model beast,
Defunct ten million years at least."

2. Extent of the Cord

In a typical human adult the nervous part of the cord from the level of the foramen magnum of the skull to the beginning of the non-nervous filum terminale, reaches only about eighteen inches, or to near the level of the first lumbar vertebra. Thus the entire axial central nervous system, including the brain and the functional part of the cord, extends only from the region of the forehead to the "small of the back." Embryonically as well as phylogenetically the cord is originally practically as long as the backbone itself.

In *Ornithorhynchus* and a few rodents it reaches as far as the sacrum, but there is a pronounced evolutionary tendency for it to shorten.

Among insects the process of cephalization, or shrinkage in the length of the cord, is very striking. The "lower" insects have a primitive nerve chain extending along the entire floor of the body, whereas "higher" forms present a condensed cord, composed of ganglia that have telescoped together into compact masses. During the metamorphosis of an insect, such as a honey bee for example, a ganglionic chain stretches the whole length of the long larval body, but in the adult worker bee, which eventually emerges from

the larva, the nerve chain is represented by ganglionic masses that are drawn much more closely together (Fig. 606).

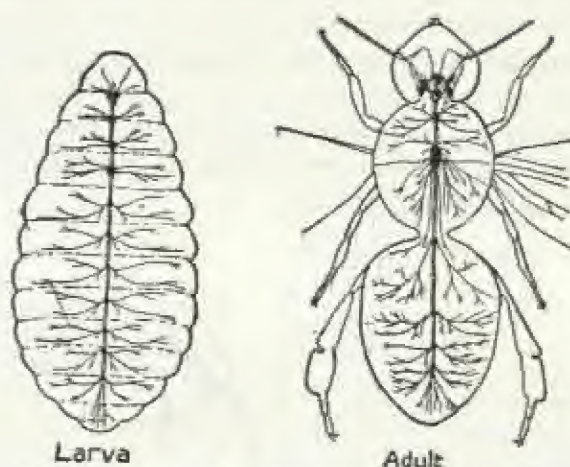


Fig. 606. Nervous system of a honeybee, larva and adult, compared to show the concentration of ganglia. (After Blanchard.)

In primates the degree of shortening marks the relative position in animal aristocracy which each form occupies, as the following table shows:

Lemur, cord ends at the	7th lumbar vertebra		
Marmoset (<i>Hapale</i>)	" "	6th	" "
Monkey (<i>Macacus</i>)	" "	4th	" "
Man	" "	1st	" "

It is interesting to speculate as to the possible fate of the shrinking nerve cord in the far distant future. Probably the time will never come when the cord will be entirely dispensed with, since there must always remain a structure of sufficient length to furnish a point of departure for the nerves supplying the body.

3. Spinal Nerves

In man there are typically 31 pairs of spinal nerves, as follows: *cervical*, 8; *thoracic*, 12; *lumbar*, 5; *sacral*, 5; and *caudal*, 1. The total number of spinal nerves in vertebrates other than man is naturally subject to wide variation.

Each pair of spinal nerves, with the exception of the cervical ones, takes its name from the vertebra just anterior to its exit. The reason for a reversal of designation in the cervical nerves is that the first pair emerges between

the skull and the first cervical vertebra, or *atlas*, and so, having no vertebra in front of it, takes its name from the vertebra immediately behind it. This method of nomenclature is followed throughout the cervical series, leaving the eighth pair of nerves without any cervical, vertebral godfather standing behind it, and accordingly it is called the eighth pair, although mammals have only seven neck vertebrae.

The next pair of nerves plainly belongs to the trunk, and so begins a new series as the *first thoracic pair*, taking its name from the vertebra *behind* which it emerges (Fig. 607).

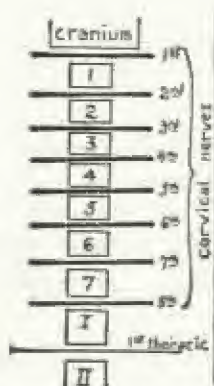


Fig. 607. Diagram showing the relation of the cervical nerves to the cervical vertebrae.

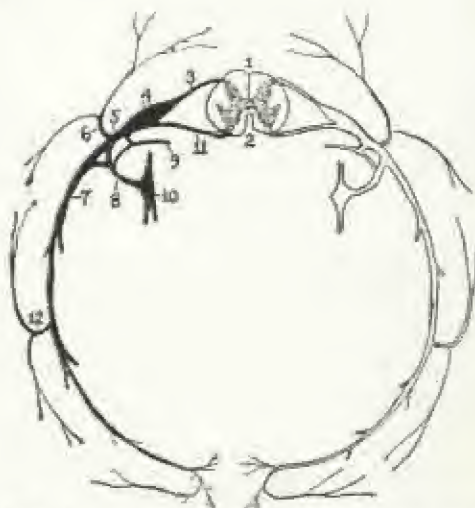


Fig. 608. Cross section of the central and peripheral nervous systems in man. 1, dorsal fissure and septum of nerve cord; 2, ventral fissure; 3, dorsal root of spinal nerve; 4, dorsal ganglion; 5, spinal nerve; 6, dorsal branch of the nerve; 7, ventral branch; 8, autonomic branch; 9, meningeal branch; 10, sympathetic chain ganglion; 11, ventral root; 12, cutaneous branch. (After Rauber.)

The size of the spinal nerves is dependent upon the relative area of the body which they supply, the largest in man being the first sacral pair that goes to the legs. The general distribution of every spinal nerve in connection with the region which it supplies is indicated in Figure 608.

The relation between the spinal nerves and the metameric embryonic muscles is very regular and constant, but the rearrangement and migration of these muscles in the adult organism brings about apparent irregularities. A nerve once associated with a muscle, however, remains faithful to it

throughout all its subsequent transformations. Since metameric muscles in mammals do not extend to a tail, as in fishes and urodeles, decided differences in the abundance of post-anal spinal nerves appear in the higher vertebrates.

In man particularly, the nerve cord is shortened as already described, so that it does not extend through the entire length of the vertebral column. Nevertheless the emerging spinal nerves maintain their proper intervertebral

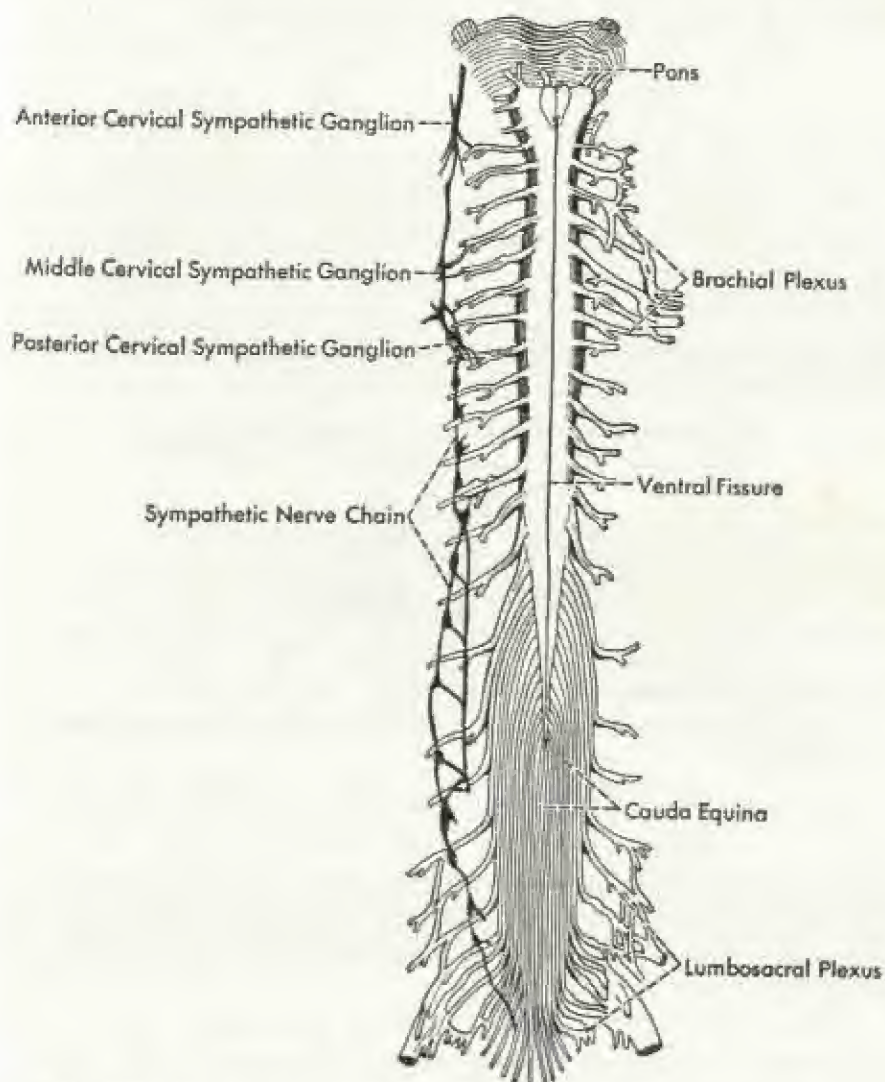


Fig. 609. The spinal cord of man, showing plexi, cauda equina, and, on one side, the sympathetic nerve chain. (After Rauber.)

exits. This necessitates the continuation of the posterior pairs of spinal nerves within the neural canal of the vertebral column for increasingly lengthened distances before they finally emerge, with the result that a brush of spinal nerves, the *cauda equina*, or the "horse's tail," is formed at the end of the cord (Fig. 609). Moreover, while the anterior spinal nerves leave the cord at practically right angles, the angle of departure for posterior pairs becomes more and more acute, until it may be said of the sacral nerves that for some distance they run almost or quite parallel to the *filum terminale*, that is, to the non-nervous continuation of the cord itself.

(a) **Roots.**—The connection between the peripheral nervous apparatus and the central nervous system is effected on either side through the dorsal and ventral roots of the nerves (Fig. 608), which differ not only in structure and function, but also in their origin and manner of development.

Dorsal roots are composed primarily of neurons whose polarity is *afferent* or *centripetal*, that is, toward the central nervous system. *Ventral roots*, on the contrary, are *efferent*, or *centrifugal*, carrying messages outward to glandular or muscular effectors. Since these effectors, which are mostly muscular, bring about motion, the ventral roots are commonly designated as "motor roots" (Fig. 610).

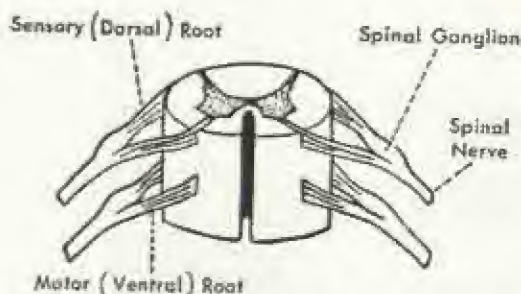


Fig. 610. Diagram of the relation of spinal nerves to the cord. (After Pierson.)

For the most part dorsal roots are made up of fibers from neurons apparently unipolar, although in reality bipolar, located in the dorsal ganglia, whose origin from the neural crests has already been described. Neurites in the ventral roots, on the other hand, which have no ganglia, take their origin from cell bodies grouped together in the gray matter of the ventral area of the cord.

Among lower vertebrates, dorsal roots in some instances are not always purely sensory but may also contain efferent fibers going to the autonomic system. A few recurrent sensory fibers also may find their way from the dorsal to the ventral root, thus modifying the character of the motor roots.

The spinal nerves of amphioxus show several primitive features. The dorsal root is mixed, including visceral (autonomic) motor fibers as well as the usual complement of sensory elements. No dorsal ganglion is present, the sensory neurons having their cell bodies in the dorsal part of the cord. Further the dorsal and ventral roots, alternating in their attachment to the cord, do not unite into a spinal nerve.

In cyclostomes the dorsal roots are also mixed and alternate with the ventral roots, but, in contrast with amphioxus, the cell bodies of their sensory fibers are located in dorsal ganglia, as in all other vertebrates. In the myxinoids (but not in the lamprey eels) the two roots join to form a united spinal nerve as in all gnathostomes. The combined spinal nerve, therefore, probably represents a secondary evolutionary adaptation.

The dorsal and ventral roots in elasmobranch fishes also emerge from the cord alternately. The dorsal root makes an intervertebral exit, through the intercalary plate, while the ventral root comes out vertebrally through a foramen which penetrates the neural plate (Fig. 432A). They then join to form a spinal nerve. In higher vertebrates both roots of a spinal nerve emerge intervertebrally in the same transverse plane.

In fishes the dorsal ganglia and the point of union of the roots of the spinal nerves are usually located outside the vertebral column, but in other vertebrates the junction of the roots is effected closer and closer to the cord itself, so that it comes to lie within the neural arch (Fig. 611).

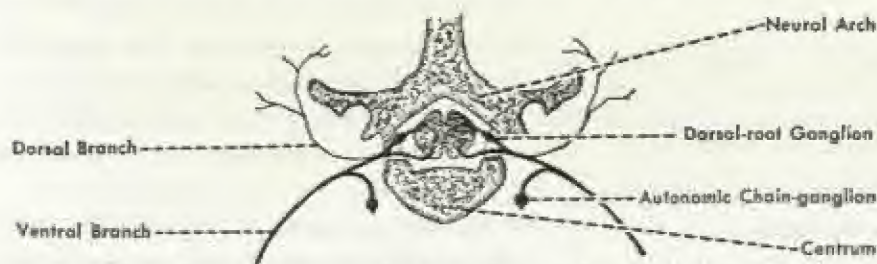


Fig. 611. Diagrammatic section through a vertebra at the level of the roots of a spinal nerve, showing the position of the spinal (dorsal-root) ganglia with reference to the vertebra. (After Jammes.)

(b) **Branches.**—Near the junction of the two roots the spinal nerve divides into four branches, or *rami*, namely: (1) a thinner, shorter *dorsal branch*, supplying epaxial sense organs, musculature, and glands; (2) a thicker, longer *ventral branch*, to similar hypaxial parts; (3) a small *meningeal branch*, going back into the neural canal to supply the blood vessels of the cord and its membranes; and (4) an *autonomic branch*, communicating with the autonomic nervous system (Fig. 608).

The important generalization that the *branches* of spinal nerves are mixed, while their *roots* are not, was independently established over a century ago by the Frenchman Magendie (1783–1855) and by Sir Charles Bell (1774–1842), an Englishman, who has been characterized by Professor Keith as “an anatomical detective of the highest rank.”

(c) **Plexuses.**—Whenever an extra large area of the body, such as that of the arms or legs, is to receive a nerve supply, several spinal nerves may join forces, forming a *plexus*. A complication of this kind adds materially to the difficulty in precisely tracing out the actual path and sequence of

neuronic lines between the central nervous system and specific end organs. It has been shown, however, that each muscle may be excited by several nerves, while any single spinal nerve may in turn affect several muscles.

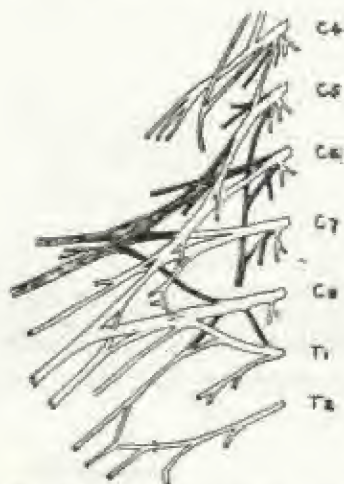
The first four cervical nerves in man form the *cervical plexus* that supplies the neck. The last four, together with the first and usually the second thoracic nerve, make up the *brachial plexus* of the arm (Fig. 612). Most thoracic nerves do not ordinarily enter into plexus formation. The twelfth thoracic, all five lumbar, and the first three or four sacrals become involved in the large *lumbosacral plexus* which supplies the leg.

In all of these plexuses only ventral rami are concerned, including both sensory and motor fibers.

Fig. 612. Diagram of the right brachial plexus of man, viewed from the front. The shaded strands are derivatives of the dorsal half of the plexus. c, cervical nerves; t, thoracic nerves. (After Eisler.)

In various species of long-bodied fishes and urodeles, which do not use their paired appendages for the support of the body, there frequently occurs, anteriorly and posteriorly along the backbone, a shifting of the girdles and their attached appendages (particularly the pelvic girdle), with a consequent variation in the group of spinal nerves that take part in plexus formation. DeBeer records this fact by saying “Limbs may become transposed over the trunk of the animal much as a tune can be transposed over the keys. But it is the same tune and the same limb.”

There are many variations in the composition of spinal plexuses in vertebrates other than man, in which the legs and arms assume particular importance. In such instances the anastomoses may even be unlike on the



two sides of the same individual. In the enormous brachial plexus of the skate, twenty-five spinal nerves may fuse together, while in certain other elasmobranchs as many as three occipital nerves may join with spinal nerves to form a *cervicobrachial plexus*. In the long-necked swan the first spinal nerve to join with another in the brachial plexus is the twenty-second.

Certain snakes (Fig. 613) in which no trace of limb-buds appears in the embryo (Fig. 614), possess a lumbo-sacral plexus, indicating that these highly modified, limbless reptiles were derived from ancestors with legs at some time in the remote past.



Fig. 613. Pelvic nerves of a snake, showing a simple plexus in the absence of hind legs. (After Carlsson.)



Fig. 614. The limbless embryo of a snake, 3.5 mm in length.

4. Development of the Spinal Cord

With the formation of the medullary tube there are established around the central canal, above and below, *roof* and *floor plates*, respectively, which do not increase notably in thickness, and two sides that enlarge enormously until they overshadow both roof and floor (Fig. 615).

In early stages there are two types of cells in the wall of the medullary tube, namely, *germinal cells*, near the central canal, and *spongioblasts*, extending from the canal to the outer surface of the cord. Soon several additional types appear, namely, non-nervous *ependymal cells*; non-nervous *neuroglia cells*; and *neuroblasts*, destined to become the important *neurons*. Germinal cells may give rise to any of these five types with the possible exception of ependymal elements, while spongioblasts differentiate into neuroglia and ependymal cells.

Three zones may now be recognized in the wall of the medullary tube, especially in its thick lateral regions, namely: (1) an inner *ependymal layer*, bordering directly on the central canal; (2) a middle *mantle layer*, containing many nuclei; and (3) an outer *marginal layer*, practically devoid of nuclei (Fig. 615).

The spongioblasts, with the ependymal cells, form a supporting framework which extends through all three layers. Although the ependymal cells are concentrated in the inner layer, they send long slender processes to the outer surface of the cord. The spiderweb-like neuroglia cells form a supporting meshwork in the middle and outer layers.

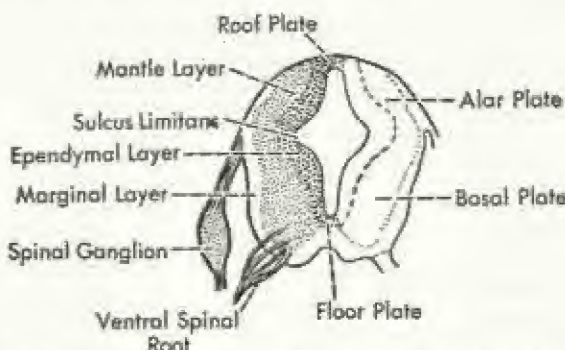


Fig. 615. Transverse section through anterior cervical region of spinal cord of a 10 mm human embryo. (From Ranson and Clark, *The Anatomy of the Nervous System*, copyright 1947, by permission of W. B. Saunders Company, publishers. After Prentiss.)

Germinal cells are especially abundant within the sustaining neuroglial network of the mantle layer where they divide repeatedly to produce larger numbers of neuroblasts. The thickening of the mantle layer, due to this rapid cell proliferation, is most marked in two regions on each side of the cord, one dorso-lateral forming the *dorsal horn*, the other ventro-lateral, the *ventral horn* (Fig. 616).

Many neuroblasts, when they begin to sprout, send their nerve fibers into the marginal layer. At first these fibers are naked but gradually myelin sheaths are added, probably through the activity of certain neuroglia cells which become temporarily associated with the fibers but do not remain to form a neurolemma. This massing of myelinated fibers in the marginal layer converts it into *white matter* in contrast with the middle layer, composed chiefly of neuroblasts, cell bodies of neurons and neuroglia, which remains *gray matter*. Eventually the inner zone becomes reduced to a thin ependymal layer lining the central canal.

Neurons of the ventral gray matter also send out neurites which establish the ventral roots of the spinal nerves and continue into the several branches. Along with the fibers go non-nervous cells which give rise to the two sheaths, myelin and neurolemma. At the same time neurons in the dorsal ganglia are sprouting. Their dendrites, accompanied by sheath cells, grow out through

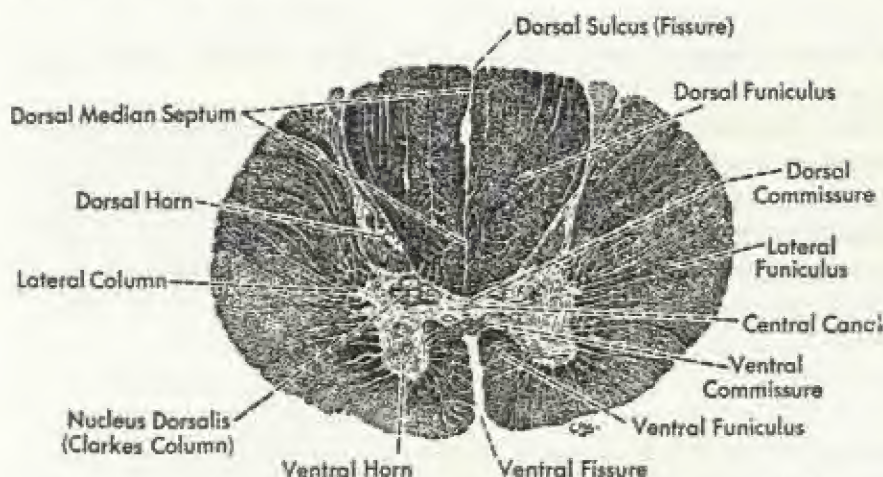


Fig. 616. Cross section through the fourth thoracic segment of the human spinal cord. (From Kappers, Huber and Crosby, *The Comparative Anatomy of the Nervous System of Vertebrates, including Man*, copyright 1936, by permission of The Macmillan Company, publishers.)

the several branches of the spinal nerves to the surface of the body or to the internal organs. Their neurites complete the dorsal roots and extend into the cord where many of them grow forward to the brain by way of the dorsal part of the white matter. These myelinated neurites also have a neurolemmal sheath up to the point where they enter the cord.

Thus the *alar plate*, the dorsal part of the lateral wall of the cord, is given over to cells and fibers of *afferent*, or *sensory*, *neurons*, concerned with bringing in impressions from without, while the ventral part, or *basal plate*, becomes headquarters for *efferent*, or *motor*, *neurons*, that convey messages outward to various effector mechanisms.

As the sensory fibers enter the cord those from the outer surface of the body, *somatic sensory component*, are more medial than those from the internal organs, *visceral sensory component* (Fig. 617). In like manner the cell bodies of the *somatic motor component*, which supplies the voluntary muscles, are in the more medial ventral horn while those of the *visceral motor component*, running chiefly to the autonomic nervous system, are in the *lateral column*, the more lateral part of the gray matter of the basal plate. Thus the gray matter includes

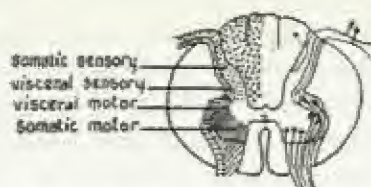


Fig. 617. Diagrammatic transverse section through the human spinal cord, showing the location of the four types of neurons in the gray matter. (After Herrick.)

four kinds of neurons, or components, in sequence from dorsal to ventral as follows: somatic sensory, visceral sensory, visceral motor, somatic motor.

In cross section the nerve cord at first has an oval outline, while the central canal appears like a dorso-ventral slit (Fig. 615). With the formation and enlargement of the ventral horns, together with the addition of the surrounding white matter, the cord bulges ventrally on either side of the thin floor plate leaving a median longitudinal groove, the *ventral fissure* (Fig. 616). The formation of less extensive dorsal bulges results in a shallow *dorsal fissure*. Further the two sides of the dorsal part of the central canal grow together, giving rise to a *dorsal median septum*, composed of ependymal cells, which extends from the bottom of the dorsal fissure nearly to the central canal. The septum is separated from the canal by a thin sheet of non-myelinated nerve fibers which grow across between the gray matter regions of the two sides, forming the *dorsal commissure*. A somewhat similar cross connection between the two sides of the cord is found ventral to the canal, but this *ventral commissure* consists of a white portion, next to the ventral fissure, in addition to the gray part near the canal.

Thus the nervous elements of the two sides of the cord are almost completely separated from one another, dorsally by a fissure and septum, ventrally by a fissure. Only the commissures act as nervous bridges between the two sides.

5. Internal Architecture of the Adult Cord

In cross sections of the fully formed cord the gray matter somewhat resembles a butterfly, or a capital letter H with a hole (the *central canal*) through the center of the crossbar (the *gray commissures*). On each side the projecting horns of the gray matter, the upper and lower parts of one upright of the letter H, separate the white matter into three large masses, the *dorsal*, *lateral*, and *ventral funiculi*. These funiculi are further differentiated into parallel *tracts*, or *fasciculi*, each of which is a group of fibers of common function and with their cell bodies in the same general location. These fibers arise from cell bodies located (1) in the dorsal ganglia; (2) in the cord itself; and (3) in the brain. Together they constitute path-ways of communication between more or less distant parts of the entire body.

The determination of the facts now known concerning these tracts has been a difficult though fascinating work, engaging many different investigators over a long period of time. Nevertheless our knowledge in these matters is all too limited. In tracing the course of the path-ways over which the countless messages of communication go, workers have employed four

outstanding methods, namely, Wallerian degeneration, study of pathological changes, observation of the order of myelinization, and electrical stimulation.

As long ago as 1852 Waller found out that when a fiber is cut the part of the individual fiber separated from the nucleus degenerates. This serves to indicate in which direction the nucleus of a nerve cell is situated. Animals whose nerve fibers have been allowed to degenerate following a particular type of cut are observed for motor paralysis, loss of sensation, or both, in any region of the body. These experiments reveal the nature of the fibers involved, the location of their cell bodies and the region or regions of the body which they supply. This type of research is aided by methods of differential staining which render fibers and sheaths visible.

Pathological conditions, especially in man, furnish similar information. Cadavers of individuals who have suffered either loss of sensation or motor paralysis during life may, upon autopsy, reveal what group of cell bodies or fibers was concerned with the symptoms.

Another method (Flechsig's) of determining the course and direction of fiber groups is dependent upon the fact that the nerve fibers, which are at first naked, do not all acquire their medullary sheaths at the same time. Because most of the fibers belonging to any one tract tend to myelinate concurrently, it is possible to recognize different pathways by this means.

The fourth method, employed considerably in recent years, involves the use of electrical stimulation. Minute electrodes are used to stimulate a limited group of nerve cells in anaesthetized animals. After tabulation of the effects produced in numerous experiments of essentially one type, it is possible to determine at least some of the connections of the stimulated areas. By this means it has been possible to obtain detailed information concerning many complicated pathways, especially those in which only a few or scattered fibers are involved and therefore other methods do not succeed.

Thus the details of the invisible individual highways of the nervous system have been pieced together accumulatively, until now quite a complete picture of the whole complicated system of nervous traffic lanes is available. As would be expected, the various paths in the Great White Way of the nerve cord are much more definite and have been more thoroughly studied in higher groups than in lower vertebrates. Representative tracts, as found in man, may be grouped as follows:

I. Ascending (Sensory) Tracts

1. Dorsal Columns

Fasciculus gracilis (Tract of Goll)

Fasciculus cuneatus (Tract of Burdach)

2. Spinocerebellar System
 - Dorsal spinocerebellar tract
 - Ventral spinocerebellar tract
3. Spinothalamic System
 - Lateral spinothalamic tract
 - Ventral spinothalamic tract

II. Descending (Motor) Tracts

- Fasciculus corticospinalis lateralis (Crossed pyramidal tract)
- Fasciculus corticospinalis ventralis (Direct pyramidal tract)

III. Association Tracts

- Fasciculus proprius dorsalis (Dorsal ground bundle)
- Fasciculus proprius lateralis (Lateral ground bundle)
- Fasciculus proprius ventralis (Ventral ground bundle)

(a) **Ascending Sensory Tracts.**—The fibers which give rise to the so-called *dorsal columns* are neurites coming from cell bodies located in the dorsal ganglia of the spinal nerves, outside of the cord. As they come into the cord by way of the dorsal root of the spinal nerve, they branch and go both anteriorly and posteriorly, with the longer branch toward the head, and the shorter branch away from the head. Both the longer ascending craniad fibers and the shorter descending caudad fibers send off collaterals that enter the gray matter, where they form synapses with either intermediate neurons or motor neurons. Many of the cranially directed fibers reach without relay as far as the brain itself.

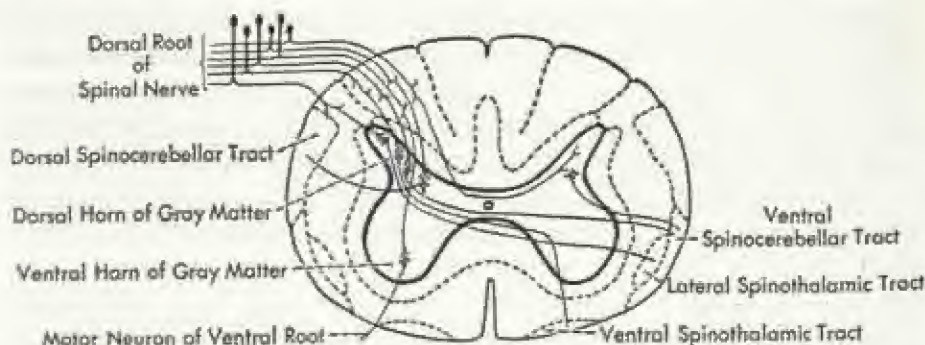


Fig. 618. The various central connections, within the cord, of sensory neurons. (After Ranson.)

Thus a neurite entering the cord through a dorsal root makes numerous central connections many of which are through its large number of collaterals (Fig. 618). Some collaterals terminate in the ventral gray matter

where they synapse with motor neurons which run out through the ventral roots to muscles or to the autonomic nervous system. Other collaterals, ending in the dorsal gray matter, synapse there with intermediate neurons, the cell bodies of which are in this part of the gray matter. The neurites of these intermediate neurons usually run into the white matter where they may enter one of several tracts, either ascending or association. Still other collaterals run through the dorsal commissure to end in the dorsal gray matter of the opposite side of the cord.

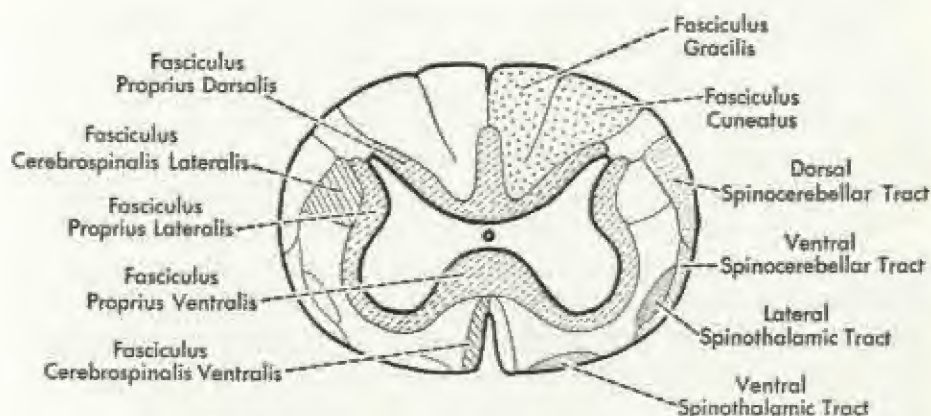


Fig. 619. The principal tracts of the cervical region of the human spinal cord. (After Ranson.)

The *fasciculus gracilis* and *fasciculus cuneatus*, which make up most of the dorsal funiculus, are composed mainly of ascending branches of the neurites of sensory neurons (Fig. 619). Fibers from sacral, lumbar, and lower thoracic spinal ganglia form the *fasciculus gracilis*, while those from anterior thoracic and cervical ganglia constitute the *cuneatus*. In the cervical region these two tracts are separated from one another by the *dorsal intermediate septum*. The courses which these and other tracts take upon entering the brain will be considered later. Although some of the short descending branches of the sensory neurons may also run in these two tracts, most of them take other pathways.

Some of the intermediate neurons with which the collaterals synapse, as mentioned above, run into the spinocerebellar tracts, located chiefly near the surface of the cord in the lateral funiculus. The *dorsal spinocerebellar tract* arises from cell bodies located in the dorso-median gray matter (*nucleus dorsalis*, sometimes known as *Clarke's column*) of the same side of the cord. The cell bodies of the fibers making up the *ventral spinocerebellar tract* are

found in the dorsal and intermediate gray matter, of the opposite side of the cord as well as the same side.

Other intermediate neurons, with which collaterals join in the dorsal gray matter, run through the ventral white commissure to enter the spinothalamic tracts, which are therefore crossed tracts, being composed of fibers which have their cell bodies on the side opposite that in which they run. The *ventral spinothalamic tract* is at the surface in the ventral funiculus, while the *lateral spinothalamic tract* lies just medial to the ventral spinocerebellar tract.

The primary sensory neurons associated with the lateral spinothalamic tract differ in two important respects from those connected with the other tracts. First of all, they are entirely unmyelinated. In addition, they do not send branches up and down the cord but, instead, enter the gray matter almost at once to synapse with neurons of the second order whose fibers then run into the white matter where they enter the lateral spinothalamic tract.

We may further observe that of these six ascending tracts the fasciculi gracilis and cuneatus have their cell bodies in spinal ganglia, while the other four have theirs in dorsal gray matter. Also, the spinothalamic tracts and some fibers of the ventral spinocerebellar are "crossed," while the other three have their cell bodies on the same side as that in which they run.

These tracts also differ in function. Impulses from "muscular-sense" organs in muscles, joints, and tendons and those from sense organs of touch in the skin are carried by sensory fibers which run at least a short distance in the fasciculi gracilis and cuneatus. These impulses are carried to the brain through three different paths, namely: (1) the original fibers of these two fasciculi; (2) the spinocerebellar tracts; and (3) the ventral spinothalamic tract. In the case of "muscular-sense," most of the impulses going to conscious levels are carried to the brain in the original fibers, while those going to the subconscious areas of the cerebellum are transferred to the spinocerebellar tracts. Tactile impulses may also be carried long distances in the original fibers, but most of them are transferred to the ventral spinothalamic tract before reaching the brain. The pathways for sensations of pain, heat, and cold go at once into the gray matter, then across to the opposite side, and forward in the lateral spinothalamic tract.

(b) **Descending Motor Tracts.**—The *cortico-spinal system*, on the other hand, runs from the brain to the cord, constituting a motor transmission highway that reaches its highest expression in mammals. Arising from cell bodies in the cortex of the cerebrum in the anterior part of the brain, it grows down by means of neurites into the cord, eventually reaching the

ventral horn of the gray area to synapse with the neurons there whose fibers extend outward through the ventral roots of the spinal nerve to the effector mechanisms.

Not all of the cortico-spinal fibers follow the same course. Most of them, upon reaching the posterior part of the brain (*medulla*), cross over from the side of their cortical origin to enter the cord on the opposite side, forming the *crossed pyramidal tracts*, which are bordered on the outside by the spinocerebellar bundles of the lateral funiculi (Fig. 619). These tracts together form "a great motor strand which brings the spinal motor apparatus under the control of the will" (Cunningham). Other fibers, fewer in number, continue from cortex to cord on the same side of their origin, forming the *direct pyramidal tracts*, that come to lie on either side in the ventral funiculus close to the ventral fissure. These latter tracts are found in only a few mammals including the anthropoid apes and man. Just before the fibers composing them terminate, they also cross over, through the white commissure of the cord, and synapse with motor neurons of the side opposite from that of their origin, so that finally all neurons of the cortico-spinal system make connections with effector neurons on the side of the body opposite to that occupied by the cell bodies from which they originate in the brain.

Other lesser descending bundles run from different parts of the brain to the cord where they synapse with motor neurons. These tracts aid in the complicated regulation of the effectors of the body.

(c) **Association Ground Bundles.**—Earlier we described simple intrasegmental reflex arcs, limited to one segment and involving one sensory, one motor, and usually one association neuron (Fig. 596). We have also shown how intersegmental reflex arcs may extend over segments in addition to the one through which the sensory neuron entered. In the latter type neurites of the sensory neurons ran in the dorsal columns giving off collaterals at various levels. These collaterals in turn went into the gray matter to carry impulses to motor neurons either directly or through an association neuron.

Another type of intersegmental reflex arc is that in which impulses are transmitted from one sensory neuron to motor neurons in a number of segments through an intermediate neuron. A collateral from a sensory neuron enters the gray matter where it synapses with the short dendrite of an intermediate cell. The neurite of this cell runs into one of the white *ground bundles* lying immediately around the gray area. These bundles, or *fasciculi proprii*, are found in all three funiculi where they form an almost continuous layer around the gray matter (Fig. 619). A neurite entering one of these bundles splits into ascending and descending branches each of which runs for only a few segments (Fig. 620). Along their courses these fibers

give off collaterals which return to the gray matter where they synapse with motor neurons. In this manner reflex responses are spread over several segments through association neurons.

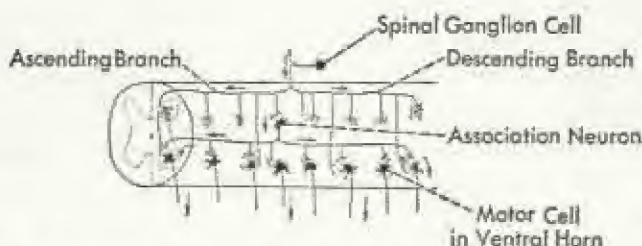


Fig. 620. Stereogram of the spinal cord showing a diffuse reflex of one side of the body, carried through fibers in a fasciculus proprius. (From Ranson and Clark, *The Anatomy of the Nervous System*, copyright 1947, by permission of W. B. Saunders Company, publishers. After Cajal.)

As in the case of intrasegmental reflex arcs and the intersegmental type in which the different levels are reached through sensory neurites, this type involving proper fasciculi is not limited to one side of the cord. Some of the intermediate fibers cross in the ventral white commissure to send impulses out through motor neurons of the side of the body opposite that to which the sensory neuron belonged. In these various ways the two sides of the body and the various segments are interconnected so that a response is by no means limited to a localized area. Under ordinary circumstances, however, the response will not be diffuse as in the case of nerve-net transmission. Instead the impulses pass along appropriate pathways as determined by synaptic connections within the cord.

It is evident from the above description that motor neurons may synapse with fibers coming from a variety of places. In fact a single motor neuron with its much-branched set of dendrites may have impulses funneled to it through several primary sensory neurons as well as by fibers from fasciculi proprii, corticospinal tracts, and other tracts which space has prevented us from discussing. As Sherrington has so aptly said, a motor neuron is "the final common path" of many reflex arcs.

Also it is evident that the cell bodies of the fibers which make up the tracts of the spinal cord have three different locations: (1) *spinal ganglia*, giving rise to the fasciculus gracilis and fasciculus cuneatus, as well as many collaterals which enter the gray matter of the cord; (2) *gray matter* of the cord, giving rise to the three fasciculi proprii (dorsalis, lateralis, and ven-

tralis), the dorsal and ventral spinocerebellar tracts, and the lateral and ventral spinothalamic tracts; and (3) the *brain*, giving rise to the crossed and direct pyramidal tracts.

The pattern of the gray and white matter, as well as the actual size of the whole cord, varies greatly at different levels in any individual. Since the white is the transmission highway between the cord and the brain, it naturally becomes cumulatively larger the nearer it approaches to the brain itself. Relative increase in the white matter at different levels within the cord of mammals is explained as machinery that makes possible more reliance on the brain in regulating the behavior of the animal.

The relative amount in square millimeters of the white and gray matter throughout the human cord is shown by the curves plotted in Figure 621.

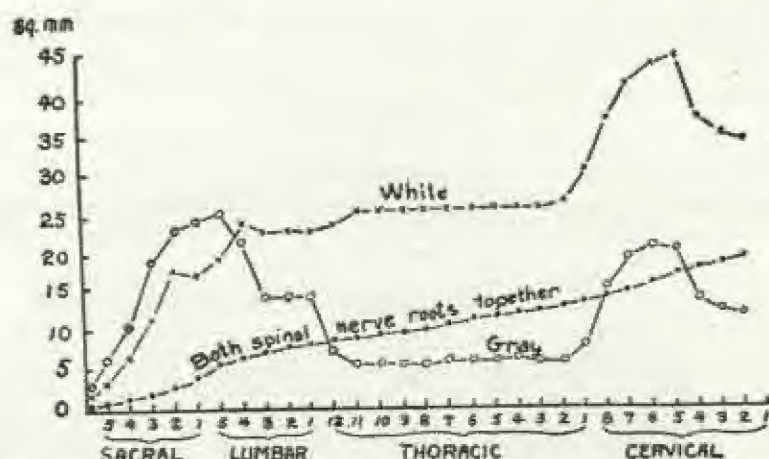


Fig. 621. Diagram showing by curves the area, at several levels of the cord, of the white and gray matter, and of the roots of the spinal nerves. (After Donaldson, compiled from measurements by Stilling.)

6. Comparative Anatomy of the Cord

The cord of amphioxus resembles that of the vertebrates in having an inner region of cell bodies outside of which are massed the fibers. The entire cord is made up of gray matter, however, as no medullary sheaths are laid down in this animal. Some of the cell bodies of sensory neurons are located in the cord, while others are distributed along the dorsal roots, never being grouped into compact spinal ganglia. The central canal is a narrow slit with only a thin roof-plate, as in vertebrate embryos (Fig. 622).

Cross sections of the broad, flat cord of cyclostomes show clearly the three zones which are typical of vertebrates (Fig. 623). The nearly circular

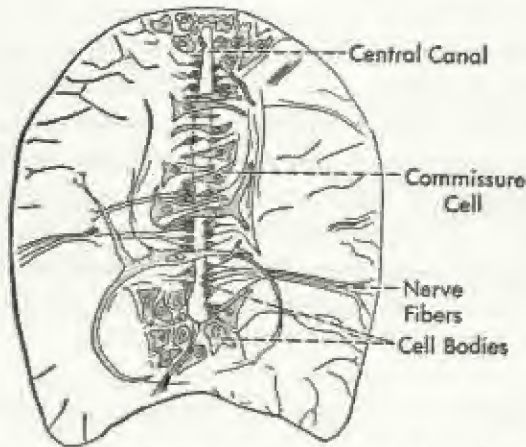


Fig. 622. Cross section through the spinal cord of amphioxus, showing locations of cell bodies. (After Franz.)

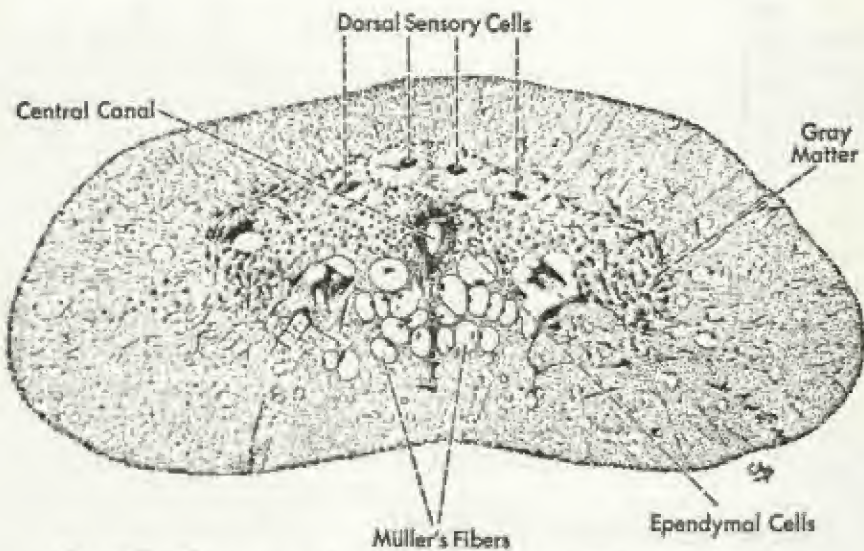


Fig. 623. Cross section through the spinal cord of *Petromyzon*. (From Kappers, Huber, and Crosby, *The Comparative Anatomy of the Nervous System of Vertebrates, Including Man*, copyright 1936, by permission of The Macmillan Company, publishers.)

central canal is surrounded by large ependymal cells. Then there is a middle zone of nerve cell bodies outside of which is a peripheral layer of fibers, non-medullated as in the case of amphioxus. The cell bodies are not confined to the vicinity of the central canal but are distributed in a broad band that extends into the lateral parts of the cord. Although the cell bodies of some

sensory neurons are located in the cord most of them are in dorsal root ganglia as in higher vertebrates. The neurites of these sensory cells run short distances in the dorsal part of the cord giving off collaterals into the gray matter. In general the cord is for local reflexes but there are a few very large motor *fibers of Müller* which run from the brain to the posterior end of the cord.

The cartilaginous fishes show definite advances toward the plan of higher vertebrates. For the first time myelinization of the fibers occurs, forming true white matter. Further the gray matter shows an arrangement into dorsal and ventral horns, although the dorsal horns are usually combined into a single broad region so that the gray matter is shaped like an inverted T rather than like an H as in mammals (Fig. 624). Instead of being arranged in compact dorsal funiculi, the sensory neurites form small bundles scattered through the dorsal gray matter. Also these sensory fibers are usually short, not extending into the brain region as they do in mammals. Compared with cyclostomes there has been an increase in the number of tracts set up between brain and cord. There are ascending fiber groups, probably corresponding to the dorsal spinocerebellar tract, as well as several descending tracts from the medulla and mid-brain.

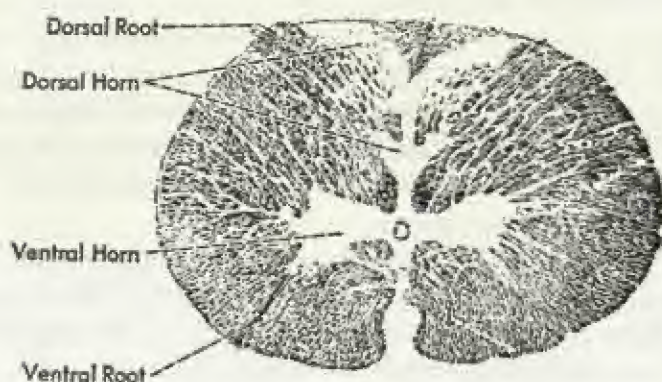


Fig. 624. Cross section of the spinal cord of a cartilaginous fish. (From Kappers, Huber, and Crosby, *The Comparative Anatomy of the Nervous System of Vertebrates, including Man*, copyright 1936, by permission of The Macmillan Company, publishers.)

The amphibians are the first to have brachial and lumbar enlargements, which make their appearance as the result of the development of the legs. As large dorsal funiculi are laid down, the gray matter assumes the butterfly shape. Various tracts have been described including the dorsal spinocere-

bellars and the probable forerunners of the spinothalamics, but the brain still exerts only limited influence upon spinal reflexes.

Reptiles have well developed brachial and lumbar enlargements except in the limbless snakes. In turtles the cord is very thin in the thoracic region, a condition probably due to the almost complete absence of thoracic musculature. Reptiles are the first vertebrates in which the dorsal funiculi carry great numbers of fibers to the brain and therefore increase in size as they go anteriorly.

The mammalian cord, unlike that of reptiles, birds, and most anamnia, never extends the entire length of the vertebral column. The great development of the dorsal funiculi, which began in reptiles, becomes progressively greater in passing from the lower to the higher mammals. The corticospinal tracts, from the cerebral cortex, are peculiar to mammals. Only the crossed tract has been described for most mammals; but the ventral, uncrossed tract is said to occur in rodents, cetaceans, and some ungulates, in addition to the primates. Although the crossed tract is ordinarily in the lateral funiculus, as it is in man, it is found in the dorsal funiculus in monotremes, marsupials, rodents, and ungulates.

VIII. MENINGES

The precious central nervous system is surrounded with wrappers of various sorts that make possible vertebral movement and turning of the head without injuring the cord or brain. The inner envelopes immediately around the cord are termed the *meninges*. In higher vertebrates there are three meninges which, from the inside out, are named the *pia mater*, the *arachnoidea*, and the *dura mater*.

The *pia mater* bears blood vessels and consequently has a nutritive mission primarily. It also carries nerves which supply the blood vessels. It fits with tailor-like snugness close around the cord and the brain, descending into the fissures and every unevenness of the surface. It has been likened to the thin, close-fitting, bitter skin around the kernel of a wrinkled walnut.

Outside the *pia* is the *arachnoid* layer, forming a spiderweb-like meshwork of great delicacy, hence its name. This is succeeded by a dense connective tissue of protective nature, corresponding to the shell of the walnut, the *dura mater*, which fits within the skeletal envelope, that is, the neural arches of the vertebrae.

In the cranium the *dura* unites with the inner periosteum (*endosteum*) of the skull bones to form a single sheet of tissue (Fig. 625). In the cord, however, it is not in direct contact with the *endorachis*, the endosteal layer

of connective tissue which lines the neural canal and lies against the inner surfaces of the neural arches and centra. Instead, dura and endorachis are separated from one another by a *perimeningeal space* filled with a fluid. In addition, the space between the dura and the arachnoid (*subdural space*),

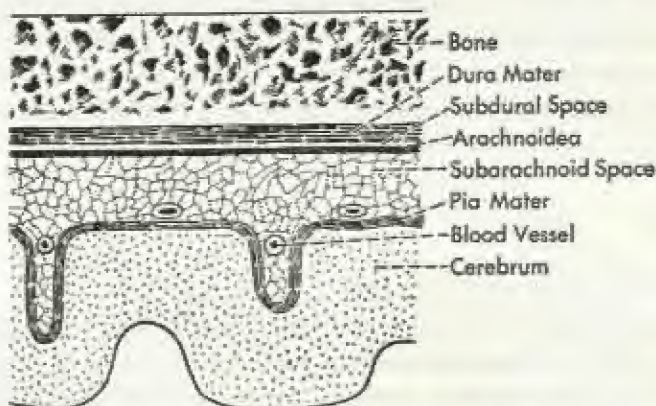


Fig. 625. Scheme of the general relations of the meninges to the brain. (After Rouvière.)

as well as that between the arachnoid and the pia (*subarachnoid space*), which is relatively of considerable size, is filled with a lymphlike *cerebro-spinal fluid*, thus forming jackets of lubricating material that serve as shock absorbers, making possible the movement of the vertebrae upon each other without causing mechanical injury to the cord.

In lower fishes there is only a single meningeal layer, the *meninx primitiva*, separated from the endorachis by perimeningeal tissue (Fig. 626A).

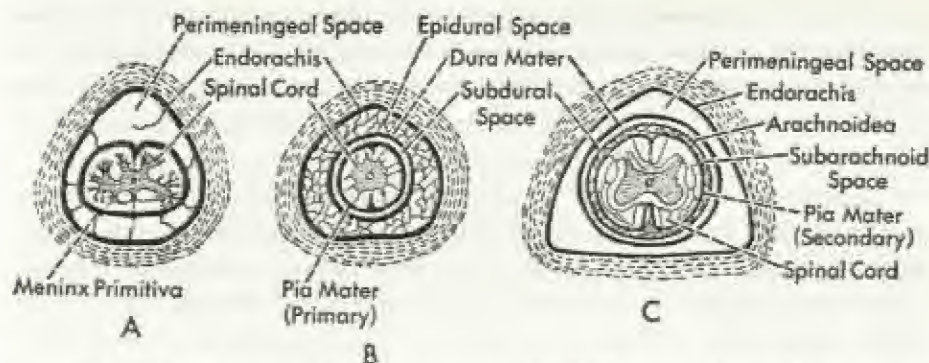


Fig. 626. Diagrams of the meninges in the chief groups of vertebrates. A, fishes; B, amphibians, reptiles, and birds; C, mammals. (After Wiedersheim and Sterzi.)

In amphibians, reptiles, and birds, the meninx primitiva becomes split into dural and pial layers, with a subdural space between (Fig. 626a), while in mammals the inner pial layer is further differentiated into the arachnoid and the pia (Fig. 626c). The complete list of envelopes of the mammalian cord from the inside out is as follows: pia mater, subarachnoid fluid, arachnoid, subdural fluid, dura mater, perimeningeal fluid, endorachis, vertebral arch, tendons and muscles, and skin. Within the cranium the endorachis and the dura are contiguous, not being separated by a fluid-filled space as in the cord region.

IX. BRAIN

1. In General

The human brain has been characterized as "nature's master contrivance," yet it must be remembered that the great majority of organisms on the earth fill out their cycle of existence, accomplishing successfully the two major activities of self maintenance and the continuation of their kind without the aid of so elaborate a mechanism as that which in man becomes the "most complicated organ known" (Minot). Nevertheless with a human brain it becomes possible to *live a human life*, which involves something more than metabolism and reproduction. This lofty goal has been gained, as comparative anatomy reveals, only after much evolutionary travail.

The vertebrate brain is the enlarged anterior end of the medullary tube. Like the cord it is a continuous tubular structure, the walls of which are composed of neurons that are arranged in communicating tracts and adjusting centers, supported and protected by non-nervous elements.

The brain became differentiated from the cord as the result of a mobilization of nerve elements in the neighborhood of the important sense organs of smell, sight, hearing, and taste, which are on guard near the entrance of the digestive canal. Whenever these sense organs are reduced or absent, as in deep-sea or cave animals, or in sessile forms, the brain diminishes in corresponding degree. Although the sense organs of the head unquestionably take a prominent part in determining the modifications which the brain undergoes, they by no means set the limit to its differentiation, for there are many animals with inferior brains whose sense organs are superior to those of man. It is primarily the *associative centers* that form the outstanding feature of the brain. Its general mass and contour, unlike that of the cord with its brachial and lumbar enlargements, are not solely dependent upon the area of stimulus-receiving surface involved, or the amount of glandular tissue supplied.

In other words, the conspicuous enlargements that characterize the walls of the brain are not so much due to incoming and outgoing limbs of reflex arcs that relate the animal directly to its environment, as to internal associative connections which, at least in man, enable the brain which "sits in darkness" not only to reconstruct the outside world but also to preserve the accumulations of memory and even to provide for creative flights of imagination.

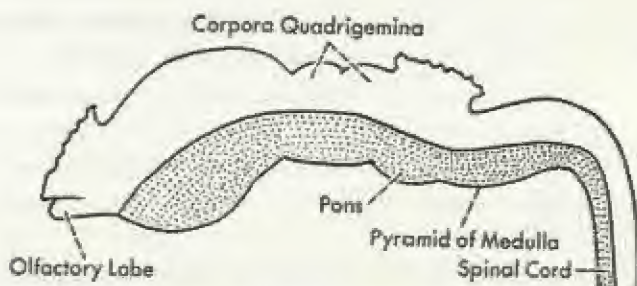


Fig. 627. Dorsal sensory and ventral motor regions of the brain stem. (After Minot.)

The primary axis, or *brain stem*, is directly concerned with peripheral nerve relations, the *motor* centers and pathways, both somatic and visceral, being located along the ventral region as in the cord, while the visceral and somatic *sensory* neurons occupy the dorsal area (Fig. 627). Upon this primary cordlike axis of simple reflex-arc systems, is superimposed the relaying association centers of correlation and coördination, the complex *cerebrum* and *cerebellum*, which are once removed from direct sense reception and muscular response. *Correlation centers* concern the adjustment of incoming sensory stimuli, while *coördination centers* regulate the outgoing motor responses. These superimposed centers of the brain may be compared to the switchboard of a telephone exchange, where messages are received and distributed.

2. Comparison of Brain and Cord

The central nervous system of amphioxus is all cord and no brain (Fig. 628). The true rise of the vertebrate brain begins in fishes, where the cord still outweighs the brain. Among amphibians the brain overtakes the cord in bulk and weight, while in modern reptiles it gets the lead, which ever afterwards in the vertebrate series is maintained.

In mammals there is an ascending dominance of the brain over the cord. A cat and a macaque monkey, for example, with cords of the same weight

(7.5 grams), have been found to have brains weighing 29 and 62 grams respectively, or ratios of 1:4 and 1:8. The ratio in man is nearer 1:50, an average measurement being 26 grams for the cord as compared with 1350 grams for the brain.

The absolute weight of the brain, it should be noted, is not in itself a reliable criterion of intelligence, since various factors, such as age, sex, form of skull, and weight of body, as well as the comparative size of different parts of the brain, must be taken into account. It is quality rather than quantity that counts.

The average human male has a brain of about 1350 grams in weight, while that of the average human female, not to start an argument but to state a fact, is something like 100 grams less. Sometimes the size of a brain is determined more by the non-nervous neuroglia cells than by the neurons.

Some notable deviations from the average weight of human brains are recorded as follows: Thackeray, the novelist, 1644; Cuvier, the comparative anatomist, 1830; Turgeneff, the historian, 2012; Haeckel, the biologist, 1575; Agassiz, the zoölogist, 1495; Schumann, the musician, 1475; Gambetta, the statesman, 1294; Whitman, the poet, 1282; Döllinger, the anatomist, 1207; and Anatole France, the writer, 1017. It is not the size of your wrist watch that is of importance, but how good time it keeps.

The weight of the brain of a dog, gorilla, and man, having approximately the same weight of body, has been found to be 135, 430, and 1350 grams respectively.

The actual mass of the human brain is exceeded among animals only by that of the gigantic elephants and whales, the size of whose body is many times that of man. An examination of the cranial cavities of the great reptiles of the Mesozoic age reveals the fact that they had insignificant brains in proportion to the enormous bulk of their bodies. Indeed it is a source of astonishment that these monsters of the past were able to get about with brains relatively so small, but it must be remembered that eventually, after an evolutionary experiment of several million years, they did succumb. It is doubtless more than a coincidence that the twilight of the dinosaurs and their reptilian contemporaries fell at about the same time as the dawn of the mammals who were at first comparatively insignificant in size, but who had



Fig. 628. Central nervous system of amphioxus, showing the alternation of the spinal nerves. Photoreceptor cells, represented by dots, are embedded in the nerve cord. (After Owsiannikow.)

a new and revolutionary ratio established between weight of brain and weight of body.

3. Differentiation of the Brain

The transforming embryonic brain is a key to the adult structure. The modification of the simple tubular brain into the exceedingly complex structure found in man is brought about through the following phases of growth: (a) constriction; (b) unequal thickenings of the walls; (c) invagination and evagination; and (d) bending.

(a) **Constriction.**—The original, somewhat inflated anterior region of the medullary tube, which is formed upon the closure of the medullary groove, is called the *encephalon* (Fig. 629A).

Very early in embryonic life (the third week in man), the encephalon becomes marked off into three regions by two constrictions (Fig. 629B). These primitive regions are designated as the *prosencephalon*, *mesencephalon*, and *rhombencephalon*, the latter so called because of the kite-shaped appearance of the ventricle, or cavity, showing here.

A little later (the fourth week in man), the prosencephalon becomes further constricted into two subregions, the *telencephalon* and the *diencephalon* (Fig. 629C). The rhombencephalon likewise (about the fifth week in man)

is subdivided into a *metencephalon* and a *myelencephalon*, the mesencephalon remaining unconstricted as it was before. The brain is now marked off into five definite areas (Fig. 629D), arranged in order from anterior to posterior as follows: telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon.

Certain of these primary regions of the brain are destined to take on special importance, because of the sense organs with which they are intimately connected. The telencephalon may be regarded as the "nose brain," the mesencephalon as the "eye brain," and the myelencephalon as the "ear brain," with the additional assignment to the latter of "skin brain" and "visceral brain."

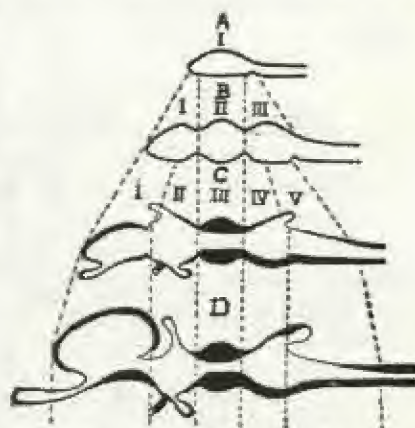


Fig. 629. Diagrams of the differentiation of the encephalon. A, primitive encephalon; B, division into an anterior prosencephalon, a mesencephalon, and a posterior rhombencephalon; C and D, further division into the five regions of the brain. (After Roux.)

Cyclostomes throughout life remain with the brain constricted into only three regions, but from fishes onward the five fundamental parts of the brain are clearly represented.

(b) **Unequal Thickening of the Walls of the Brain.**—The walls of the primitive encephalon are at first of approximately equal thickness, but as neurons develop and collect into centers and transmission tracts, the disposition of these collections of nerve elements brings about decided contrasts in the thickness of the walls of the brain in different places.

The thinnest regions are at two points, the roofs, or *vela*, (1) of the diencephalon and small median portion of the telencephalon and (2) of the myelencephalon (Fig. 630). Each velum includes only the thin endodermal layer.

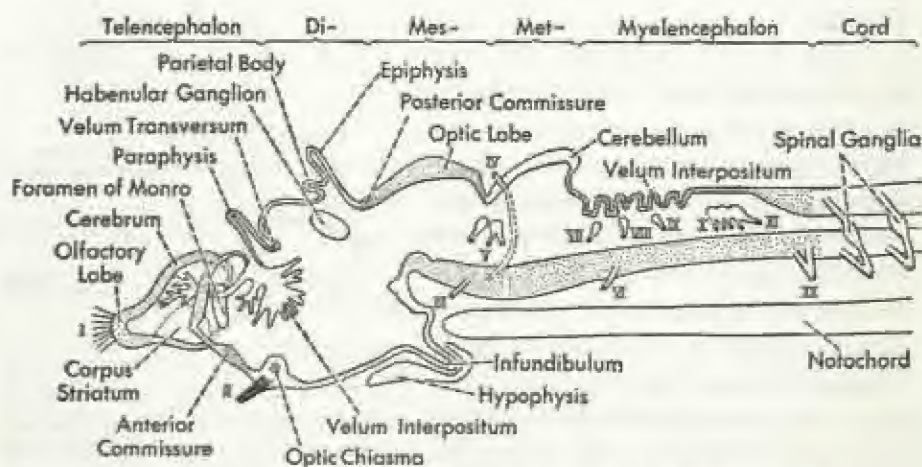


Fig. 630. Sagittal diagram through a vertebrate brain, showing the five general regions and the variations in thickness of the brain wall. Based upon the brain of a cyclostome. Telencephalon, mesencephalon, and myelencephalon stippled; other parts in outline. (After Bütschli.)

The thickest areas, on the other hand, are the *cerebellum*, which develops from the dorsal part of the metencephalon, and the walls of the *cerebral hemispheres*, the paired antero-lateral outgrowths which make up most of the telencephalon. The cerebral hemispheres, the crowning hope of the evolving brain, become so enormously thickened and enlarged in mammals that they overshadow and entirely cover up both the diencephalon and the mesencephalon, concealing them from dorsal view (Fig. 652).

(c) **Invaginations and Evaginations.**—There are two places where the brain wall is pushed in or invaginated, namely, in the regions of the thin

vela just mentioned. Over the outside of these thinnest places in the walls of the brain extends a network of capillaries in the *pia mater*, the vascular meninx that intimately envelops the brain. These capillary nets are the *choroid plexuses*, which by invagination are pushed down into the cavities of the brain below, carrying the thin wall with them. They provide a blood supply for the inside of the brain.

From the walls of the diencephalon, there also occur various *evaginations*. In certain vertebrates these are two finger-like outpushings of the wall, one behind the other, on the dorsal side just behind the invaginated choroid plexus. The anterior of these evaginations, near the junction of the cerebral hemispheres and the diencephalon, is the *parietal organ*, which is particularly developed in certain reptiles, while the posterior projection, the *epiphysis*, or *pineal "gland,"* appears in some stage of degeneration or elaboration in practically all vertebrates (Figs. 418 and 630).

A ventral median evagination of the floor of the diencephalon, the *infundibulum*, has already been mentioned. It joins a glandular upgrowth from the roof of the mouth to form the *hypophysis*, which, like the pineal body, has been briefly considered in Chapter XVI as a gland of internal secretion (Fig. 417).



Fig. 632. Diagram showing the flexures of the brain.

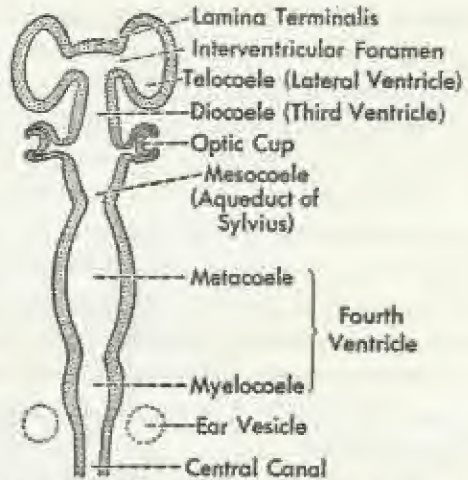


Fig. 631. Frontal diagram to show the cavities of the brain.

The *optic stalks* extending out from the sides of the diencephalon in early embryonic life are also evaginations (Fig. 631).

(d) **Bendings.**—In cyclostomes and other lower vertebrates the parts of the brain retain their primitive tandem arrangement, but with the onrush of growth and the ultimate confining limits of the skull, it becomes necessary for the brain stem to bend and fold to accommodate itself to more compact quarters. The bends, or flexures, of the brain are typically three: (1) the *parietal flexure* in the region of the mesencephalon; (2) the *cervical flexure* near the junction of the medulla and the cord, and (3) the *pontine flexure* between these two. The first two flexures bend ventrally while the

third bends in the opposite direction, thus tending to kink the brain stem together like a compressed accordion (Fig. 632).

4. Ventricles

The *central canal*, within the cord, remains very small and is approximately uniform in size throughout its length. It is the result of invagination and growth. Continuous with the central canal, and like it filled with cerebro-spinal fluid, are the cavities or *ventricles* of the brain (Fig. 631). These are chambers of unequal dimensions, and are frequently encroached upon but never entirely obliterated by the thickening walls of the brain itself.

The *fourth ventricle* is the most posterior chamber, located in the myelencephalon and metencephalon. It is roofed over by the thin velum which in ordinary dissection is frequently torn away, exposing this ventricle as a somewhat triangular trough, narrowing posteriorly to become the central canal. Anteriorly the fourth ventricle leads into the cavity of the mesencephalon, a large *mesocoel* in lower vertebrates but reduced to a slender canal, the *aqueduct of Sylvius*, when the walls of this region thicken in most higher groups.

The aqueduct communicates anteriorly with a narrow vertical slitlike *third ventricle*, the cavity of the diencephalon and small median portion of the telencephalon. Its anterior wall is the *lamina terminalis*, the anterior end of the embryonic brain, while its roof is the thin velum. The paired cerebral hemispheres, which grow laterally from the telencephalon, enclose paired cavities, the *lateral ventricles*. Each of these lateral cavities communicates with the small telencephalic part of the third ventricle through an *interventricular foramen*, sometimes called the *foramen of Monro*.

5. General Topography of the Mammalian Brain

Before considering the chief evolutionary changes in the brains of vertebrates, we may first discuss the main features of the mammalian brain, which represents the last chapter in the story but which has been more thoroughly studied than that of other animals.

The dividing point between the spinal cord and the brain is a somewhat arbitrary one, there being no sharp line of demarcation between the cord and the posterior part of the myelencephalon, or *medulla oblongata*. It is usually stated that the brain is that part of the central nervous system which is within the skull, while the cord begins at the foramen magnum, at a point immediately anterior to the first cervical spinal nerve.

Although the posterior end of the human medulla oblongata resembles the cord in both external appearance and internal features, its anterior por-

tion differs considerably from the cord, as a result of many rearrangements of parts here. The *dorsal fissure* continues forward to about the middle of the medulla where the spreading of its lateral walls, the *funiculi gracilis* and *cuneatus*, transforms the roof-plate region into a broad thin *velum interpositum* (Fig. 633). The *central canal*, which has continued into the

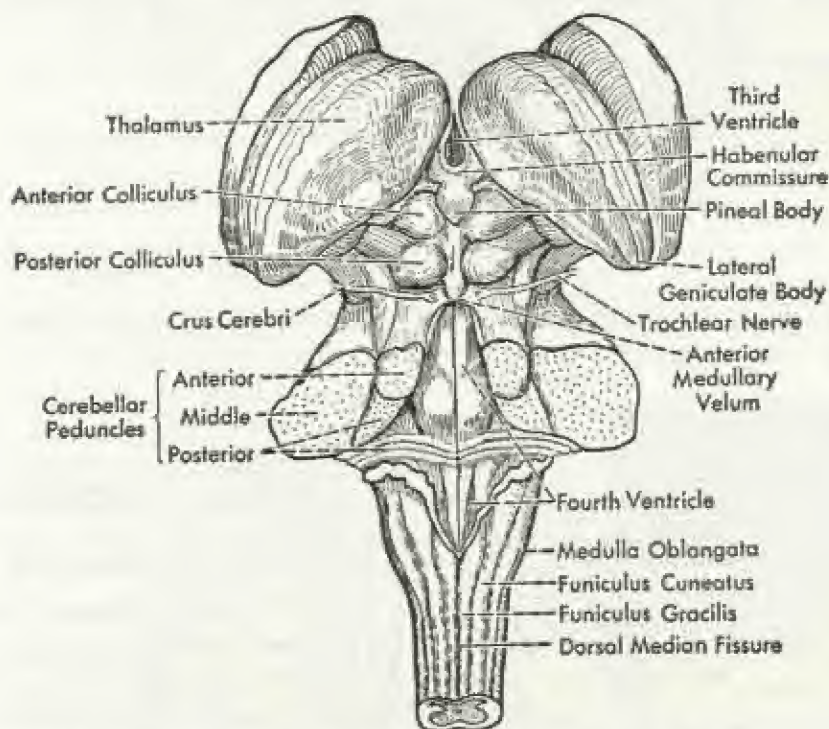


Fig. 633. Dorsal view of the human brain stem. (After Toldt.)

medulla, expands into the *fourth ventricle* as another result of the spreading of these funiculi which thus become the lateral walls of this cavity (Fig. 634). The thin velum is covered by a highly vascular pia mater from which tufts of blood vessels push into the fourth ventricle, carrying the velum ahead of them, to form the *posterior choroid plexus*. In each of the lateral walls of the ventricle, fibers continue forward to the anterior end of the medulla and then turn dorsally to enter the cerebellum. This pair of connections, known as the *restiform bodies*, or *posterior cerebellar peduncles*, is the chief pathway joining the cerebellum with the medulla and cord.

The *ventral fissure* terminates at the anterior end of the medulla (Fig. 635). Anteriorly this fissure separates two longitudinal swellings, the *pyra-*

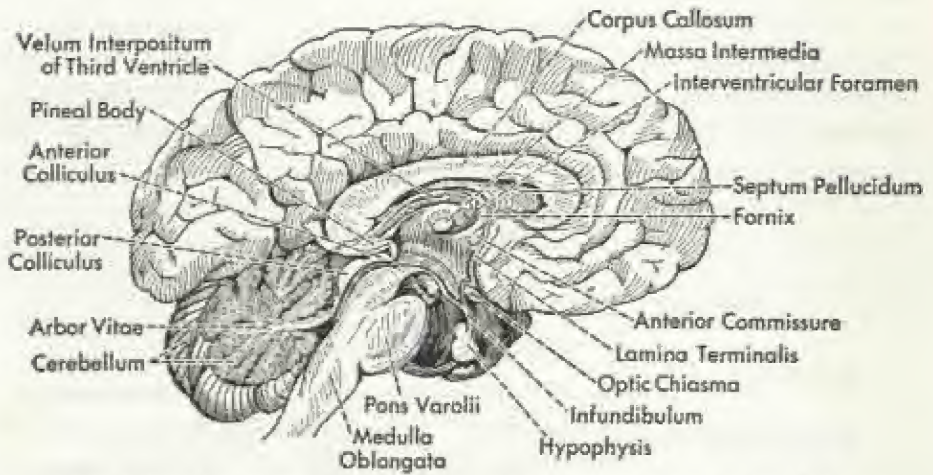


Fig. 634. Median sagittal section through the human brain. (After Toldt.)

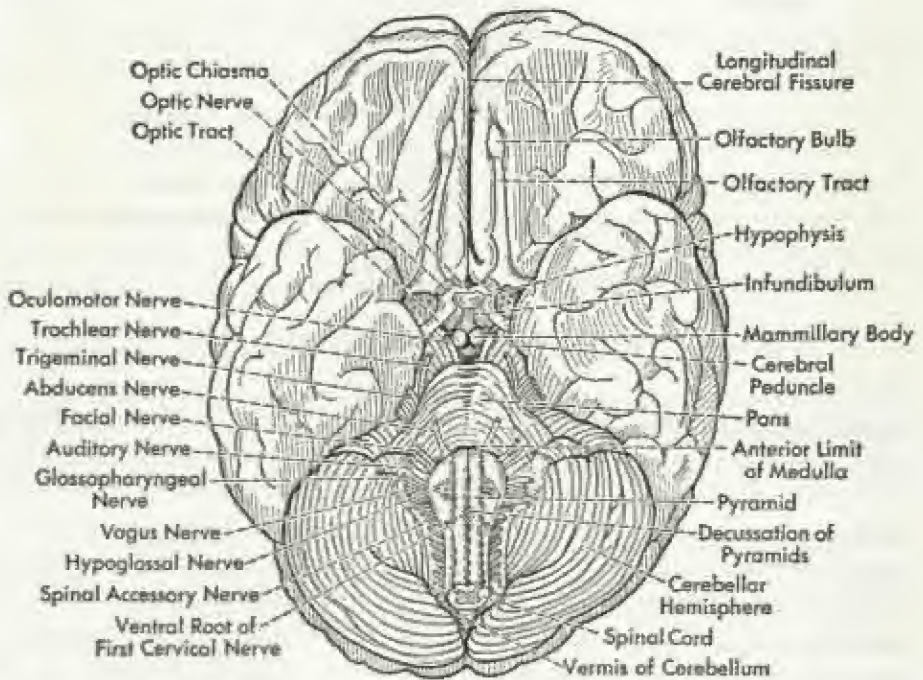


Fig. 635. Basal view of the human brain. (After Toldt.)

mids, lying side by side in the ventral part of the medulla. These structures are composed largely of the corticospinal tracts that extend from the gray matter of the cerebrum down into the cord. Near the posterior end of the medulla, bundles of pyramidal fibers cross obliquely from one side to the other, forming the *pyramidal decussation* (*decuss-*, to cross as in an X) which interrupts the ventral fissure. The fibers which cross at this point make up the *crossed pyramidal tract* of the cord. In man about one-fourth of the pyramidal fibers do not cross but continue into the cord as the *direct pyramidal tract*.

Eight pairs of cranial nerves, V–XII inclusive, connect with the mammalian medulla.

Anterior to the medulla and surrounding the anterior portion of the fourth ventricle is the *metencephalon*. The dorsal part of this region is greatly enlarged into the *cerebellum*, a structure which has been called the “gyroscope of the body,” because it is chiefly concerned with muscular coordination and maintenance of equilibrium. The cerebellum consists of a median *vermis*, so named because of its worm-like appearance, on either side of which is a large *cerebellar hemisphere* (Fig. 655). Within the cerebellum, the gray matter forms an outer layer, the *cerebellar cortex*, covering over the inner white matter. In longitudinal sections, particularly those through the vermis, the white matter shows a conspicuous tree-like arrangement to which the name *arbor vitae* has been applied (Fig. 634).

Perhaps the most interesting cells in the entire brain are the *Purkinje cells* (Fig. 636), abundant in the outer part of the cerebellar cortex. Each one has two or three dendrites which branch repeatedly to form hundreds of minute fibers spreading out chiefly in one plane “like the branches of a vine on a trellis,” to use Ranson’s apt comparison. Near the cell body the neurite, which leads toward the center of the cerebellum, gives off collaterals that run back toward the surface of the cortex to synapse with dendrites of other Purkinje cells, thus linking together many of these elements. These cells are of particular interest because of the part they presumably play in the coordination of the muscles.

The ventral portion of the metencephalon is the *pons*, so named because its ventral or outer part is made up of a broad “bridge” of fibers looping around between the two cerebellar hemispheres (Fig. 635). In the deeper

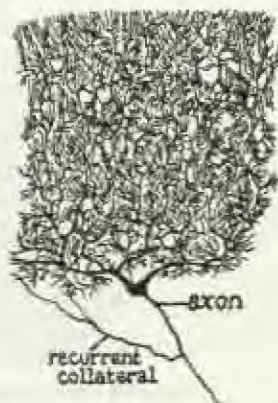


Fig. 636. Purkinje cell of adult human cerebellum, from a Golgi preparation. (After Ramon y Cajal.)

or inner part of the pons are found most of the tracts represented in the anterior part of the medulla.

The cerebellum is connected with the other parts of the brain by three pairs of structures known as *cerebellar peduncles*. The posterior cerebellar peduncles were described above as the restiform bodies which connect medulla and cerebellum (Fig. 633). The *middle cerebellar peduncles*, the largest of the three pairs in man, pass around the sides of the brain to join the pons. The *anterior peduncles* of the cerebellum run forward into the mesencephalon. Between these last named structures the roof of the fourth ventricle is again merely a thin layer of ependymal cells. This thin roof, extending from the white matter of the cerebellum forward to the roof of the mesencephalon, is known as the *anterior medullary velum* (Figs. 633 and 637). No choroid plexus is associated with this velum.

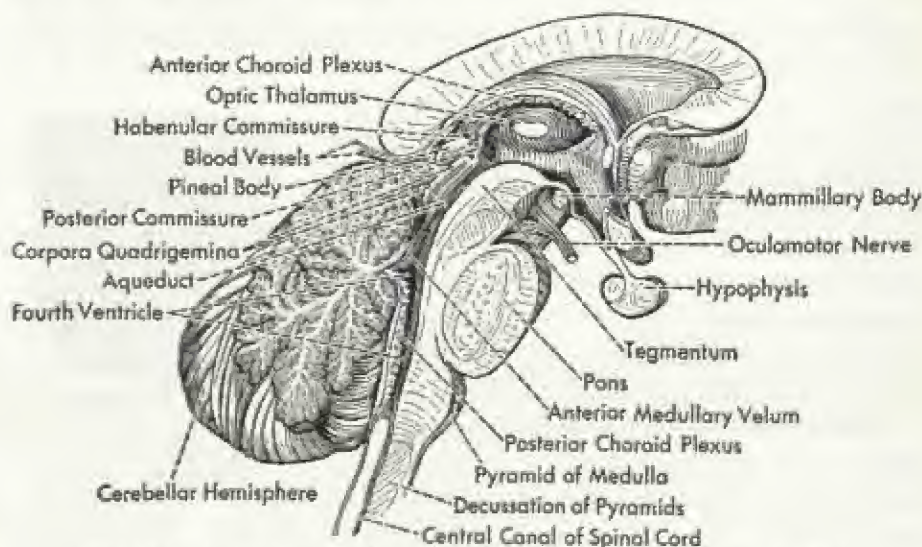


Fig. 637. Sagittal section through the human brain stem. (After Toldt.)

The mesencephalon, or mid-brain, is the most conservative region of the brain. Its walls, of moderate thickness, surround the slender *aqueduct* which connects the third and fourth ventricles (Fig. 637). The dorsal side of this region is marked by four rounded elevations, the *corpora quadrigemina*, arranged one pair behind the other (Figs. 633 and 637). The anterior ones, or *anterior colliculi*, are important reflex centers associated with visual impulses, while the *posterior colliculi* are auditory centers. The ventral surface is raised up into a pair of conspicuous rounded ridges, the *cerebral peduncles* or *crura cerebri*, arranged like a V with their converging posterior

ends passing into the pons (Fig. 635). More than half of the fibers which make up these crura belong to the corticospinal tracts. Dorsal to each cerebral peduncle the ventro-lateral part of the mesencephalon is known as the *tegmentum*, a region composed of various tracts and nuclei, including the nuclei of cranial nerves III and IV.

The diencephalon, which encloses all except the most anterior portion of the slit-like *third ventricle*, is a small but complex region composed of the following parts: (1) the *velum interpositum* of the third ventricle, a thin non-nervous portion of the roof-plate; (2) the *epithalamus*, the nervous portion of the dorsal region; (3) the *thalamus*, a large mass on each side forming most of the lateral wall of the ventricle; and (4) the *hypothalamus*, or ventral part.

The velum forms most of the roof of the third ventricle including the extreme anterior part which lies in the small median portion of the telencephalon (Fig. 637). It is covered by the vascular pia mater which sends capillary masses into the third ventricle, pushing the ependymal layer of the velum ahead of them. These capillaries, the *anterior choroid plexuses*, are not confined to the third ventricle but also extend through the interventricular foramina into the lateral ventricles of the telencephalon.

The epithalamus, the somewhat U-shaped remainder of the roof, includes the pineal body and the habenula, both of which lie just in front of the anterior colliculi, at the closed end of the U (Fig. 633). The *habenula* is made up of a pair of *habenular ganglia* connected by a bundle of fibers, the *habenular commissure*, which forms the transverse part of the "U". The habenula is an olfactory center found in all vertebrates. The *pineal body*, a small pine-cone-shaped structure attached by a short stalk to the habenular commissure, has already been considered in Chapter XVI in connection with the ductless glands.

Each thalamus is a large oblong mass including many centers, as well as bundles of fibers connecting the cerebral hemispheres with the remainder of the brain and the cord. The crura cerebri, running obliquely forward and outward to enter the cerebral hemispheres, skirt the ventro-lateral border of the thalamus.

The hypothalamus, lying between the spreading anterior ends of the crura cerebri, forms the floor and part of the lateral wall of the third ventricle. It includes the optic chiasma, tuber cinereum, mammillary bodies, infundibulum, and posterior lobe of the hypophysis. The *optic chiasma*, where fibers of the optic nerves (Cranial II) cross, is at the anterior end of the hypothalamus (Figs. 635 and 637). Immediately posterior to the chiasma is the *tuber cinereum*, an elevation to which the hypophysis (see Chapter

XVI) is attached by the funnel-shaped *infundibulum*. The *mammillary bodies*, a pair of small rounded elevations in the posterior part of the base of the *tuber cinereum*, are olfactory centers.

The telencephalon includes a small median portion and two large *cerebral hemispheres* which arise embryonically as lateral evaginations of the median region. In the median part is found the extreme anterior end of the third ventricle from each side of which an *interventricular foramen*, or *foramen of Monro*, opens into the *lateral ventricle* of the corresponding hemisphere. The anterior wall of the third ventricle is a thin membrane, the *lamina terminalis*, which marks the anteriormost part of the brain in the mid-line (Fig. 637).

Each cerebral hemisphere differentiates very early into three regions, *corpus striatum*, olfactory lobe, and *pallium*. The *corpus striatum* is the thick ventro-lateral part of the hemisphere. The *olfactory lobe*, or *rhinencephalon* (*rhin*, nose), evaginates from the cerebral floor anterior to the *corpus striatum*. The remainder of the hemisphere is the thin-walled *pallium*. As the mammalian *pallium* grows much more rapidly than the other two parts, it soon makes up most of the hemisphere, extending both anterior and posterior to the other parts as well as expanding laterally and dorsally until it meets the *pallium* of the other side, dorsal and also anterior to the *diencephalon*. Between the enlarged hemispheres there persists a narrow space, known as the *longitudinal cerebral fissure*, in which lie folds of the meninges of the brain.

The *corpus striatum* is so named because in the adult it consists of gray nuclear masses alternating with sheets of white medullated fibers. According to Ranson little is known about the function of this region.

The *pallium* includes an outer gray layer, the *cerebral cortex*, and an inner complex of white matter. In mammals only a small portion of the *pallium*, known as the *archipallium*, is associated with olfactory impulses although in lower vertebrates virtually the entire telencephalon has this function. In the cat, the *archipallium* shows on the surface of the hemispheres only as the ventral *pyriform lobe* with which are connected the *olfactory tract* and *olfactory bulb* (Fig. 638). The *olfactory nerves* (Cranial I) lead from sensory endings in the nasal cavity to the olfactory bulbs. In man the *archipallium* is even more restricted than in carnivores.

The great non-olfactory portion of the *pallium*, known as the *neopallium*, is the main center of the whole central nervous system in mammals. In the cerebral cortex of the *neopallium* are located the centers of conscious sensations and of voluntary motor control. White fibers immediately beneath the outside gray layer form an intramural network of great complexity.

connecting different regions of the cortical area with one another and with other parts of the brain forming a unifying and integrating system of supreme importance.

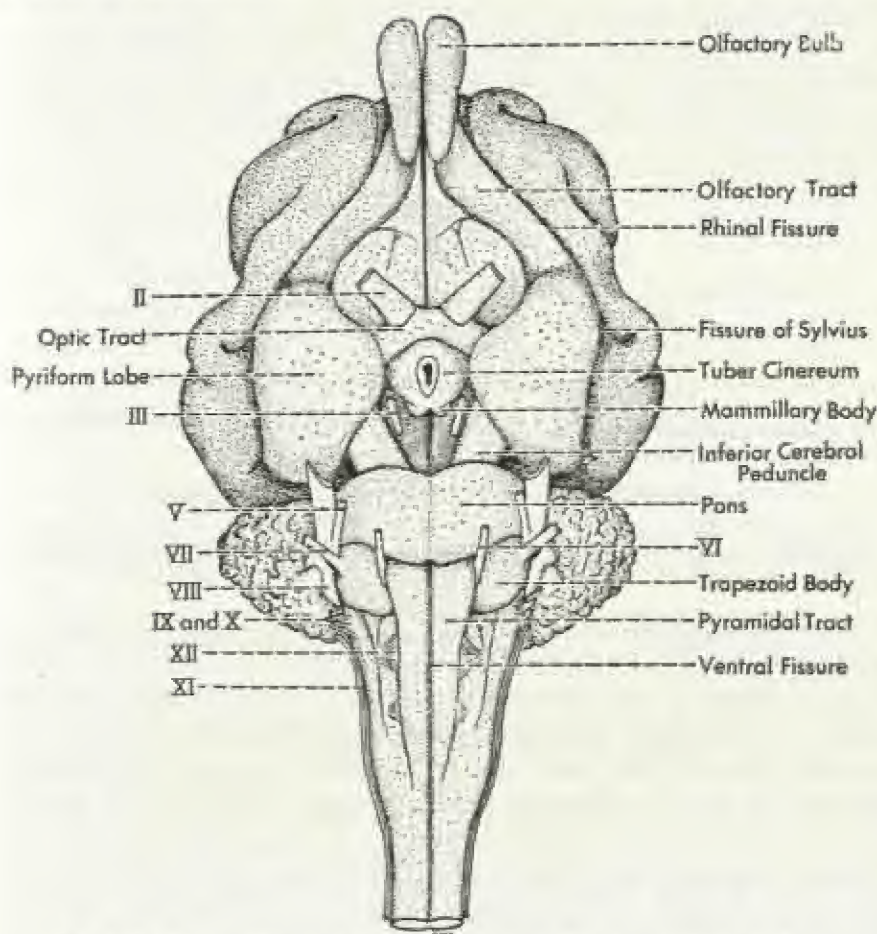


Fig. 638. Ventral view of the brain of a cat. The hypophysis has been removed. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

The two hemispheres become secondarily joined by *commissures*, transverse bands of medullated fibers. The *anterior commissure*, developing in the lamina terminalis, connects the olfactory, or archipallial, regions. The *corpus callosum*, a broad band which spreads out extensively in the hemispheres, establishes elaborate connections between their neopallial portions. Both of these parts may be seen in sagittal sections of the brain (Figs. 634 and 637). Two other portions of the telencephalon which show clearly in

such sections are the fornix and the septum pellucidum. The *fornix* is a curved longitudinal band of white fibers of olfactory function. The *septum pellucidum*, between the fornix and the corpus callosum, is a thin median wall separating the lateral ventricles. Between the two layers of the septum is a cavity which has been called the "fifth ventricle," a term which is unfortunate in view of the fact that it is not derived from the cavity of the embryonic medullary tube and hence is in no way comparable to the true ventricles of the brain.

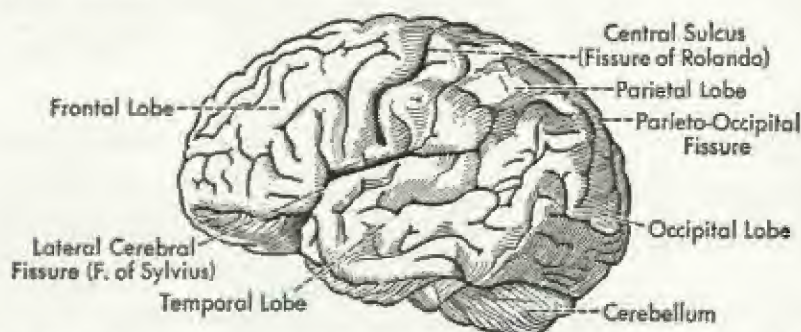


Fig. 639. Lateral view of the left cerebral hemisphere of man. (After Toldt.)

In many mammals, particularly the larger ones, the cortical surface of the cerebral hemispheres is increased by the formation of folds or convolutions, not found in monotremes, marsupials, insectivores, bats, and most rodents. The miniature mountain chains thus formed are called *gyri*, and the valleys between them, *sulci* (Fig. 639), while particularly deep sulci are designated as *fissures*. Mammals with convoluted brains have the gyri and sulci already marked out at birth. Quite contrary to prevalent opinion, their elaboration is not so much an index of intelligence as are the subcortical white fibers beneath, which make possible the innumerable conditioned reflexes that transform the cerebrum into an effective organ of integration. "The attempt to make a great deal of this feature yields but little comfort," as Stiles says, "since the sheep and cow have deeply furrowed cortical surfaces, while some apes, with much more intelligence, have nearly smooth brains."

Nevertheless the fissures do serve as boundary lines for certain regions into which the cerebrum may be parceled out topographically for convenience in localization and description. Such, for example, are the *frontal*, *parietal*, *occipital*, and *temporal lobes*, corresponding roughly to the cranial bones that cover them. The frontal and parietal lobes are marked off from one another by the *central sulcus* (*Fissure of Rolando*) while these two lobes

are separated from the temporal by the large *lateral cerebral fissure* (*Fissure of Sylvius*).

6. Cerebral Localization

A century ago two anatomists, Goll and Spurzheim, attempted to associate certain human "faculties" with definite areas in the cortex. What began on their part as a legitimate scientific inquiry and experiment, soon developed into the quagmire of *phrenology*. This pseudo-science gained great temporary vogue in the hands of clever charlatans who knew very little about the brain. Trading upon the ignorance of the general populace, wandering "Professors of Phrenology," by skillful guesswork and owlish digitation of "bumps" on the cranium, covered up their lack of real knowledge of cerebral localization and were usually able to satisfy their credulous patrons as to the great hidden capacities of any particular brain. Thus "mute inglorious Miltons" and unrecognized rural Napoleons were discovered everywhere at fifty cents a head! Today the discredited phrenologist properly belongs with the witch doctor, palm reader, clairvoyant, fortune teller, and astrologer, although it must be admitted that many of his blood relatives, who would seek a short cut to the truth that may be gained only by slow and patient travel over a long road, are still abroad and active in many guises.

There is, however, a discoverable localization of different functional centers in the cortex. This fact has been abundantly demonstrated beyond all doubt, both clinically and experimentally, as well as pathologically, by the examination of brain lesions and defects in autopsies following various types of local paralysis.

One of the earliest proofs of the cortical localization of a specific motor center was furnished during the Franco-Prussian War in 1870, when two surgeons, Fritsch and Hitzig, operating upon a wounded soldier, accidentally demonstrated a definitely located muscular response when a certain area of the exposed cerebrum was subjected to slight galvanic stimulation.

The knowledge of brain localization that has been pieced together in the last half century is of the greatest importance. By observing the part of the body that is suffering from paralysis the surgeon is able to know without preoperative exploration exactly the spot in the cortex where a blood clot, tumor, or lesion is situated.

The location of some of the cortical centers is shown in Fig. 640. It will be noted that the centers there shown do not represent mental or psychological characteristics, but instead centers of correlation, association, or projection, in direct relation to external sense organs and effectors of various

kinds. Even a process as obscure as thinking is not different in kind from other functions of the brain and may be referred in the last analysis to the operation of reflex arcs with corresponding relationships between neurons.

Although "specific mental acts or faculties are not resident in particular cortical areas," according to Herrick, yet physiological centers, definitely assigned to particular tasks, similar to the arrangement of buildings in accordance with zoning laws, have been mapped for the entire surface of the cerebrum.

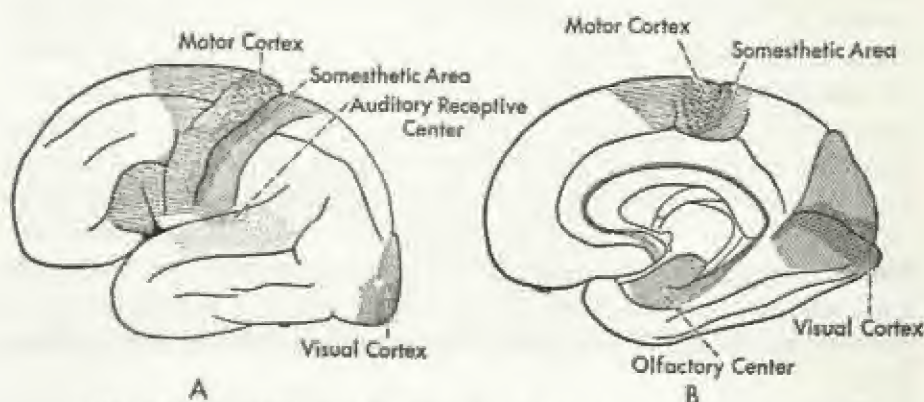


Fig. 640. Cerebral cortical areas. A, on lateral aspect; B, on medial aspect. (From Ranson and Clark, *The Anatomy of the Nervous System*, copyright 1947, by permission of W. B. Saunders Company, publishers.)

The phenomena included under the general term of *aphasia*, which may be manifested in various guises such as the loss of the power of speech (*aphemia*); the loss of ability to understand spoken words (*auditory aphasia*); the loss of ability to read printed or written language that was formerly understandable (*alexia*); or the loss of ability to write (*agraphia*), are all found to be associated with lesions or defects in definite regions of the cerebral cortex. There even seem to be different centers for different languages, since a bi-lingualist may lose by brain lesion the ability to speak one of two languages in which he was formerly proficient.

Distributed along the anterior edge of the central sulcus, on the side of the brain opposite to the region of the body involved is the *motor cortex* in which are the principal motor centers for specific regional muscles. The parts of the body are represented in inverted order, the area for the toes being the most dorsal, while those for the face are the most ventral (Fig. 641).

The left frontal lobe of the cerebrum is the location of the *speech center*

(in right-handed persons); the occipital lobe, of the *visual center*; and the temporal lobe, of the *auditory center*. All of these lobes are enlarged in connection with the power of speech with which sight and hearing are intimately associated in the case of man. Immediately posterior to the central sulcus in the parietal lobe, is the *somatesthetic* (*somesthetic*) *area*, the center for sensation of touch, pressure, pain, and temperature as well as proprioceptive sensibility from the muscles, tendons, and joints (Fig. 640). As in the case of the motor cortex the parts of the opposite side of the body are represented in inverted order with the result that the motor and sensory areas for any individual part are at the same level on either side of the central sulcus.

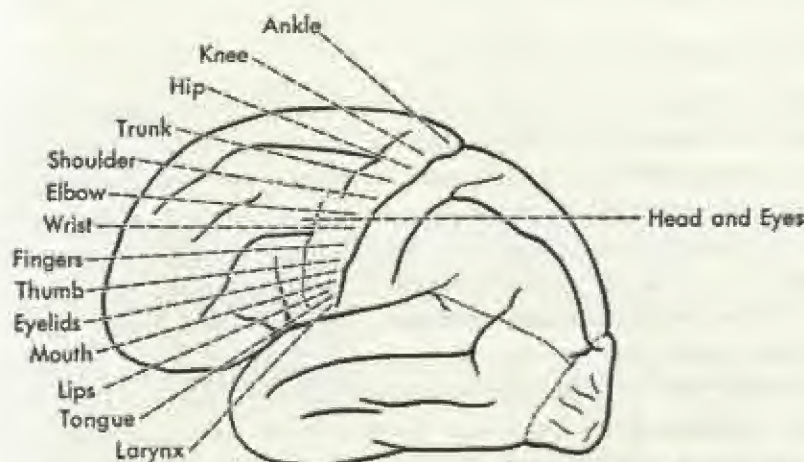


Fig. 641. Motor localization in the cerebral cortex. (From Ranson and Clark, *The Anatomy of the Nervous System*, copyright 1947, by permission of W. B. Saunders Company, publishers.)

The brain not only receives impressions through the sense organs but it also records them by means of the mechanism furnished by the cortex for storing impressions that may be later revived by memory. As has been aptly said: "When we wake in the morning the sheet of gray cortex on the brain becomes the screen on which is lit up the cinema of the outside world" (Keith). It has been estimated that the cortical fibers of a single human brain if placed end to end would reach a distance equal to that from New York to Paris, a fanciful and incomprehensible guess that probably falls short of the truth.

The billions of cells composing the gray cortex of a single human brain all together represent a mass of less than a cubic inch of material that weighs only about thirteen grams, or approximately one five-thousandth of the total

body weight. The value of this precious cubic inch of tissue is summed up by Parker * in the following words:

"When it is recalled that the 92,200,000,000 cells in the human cerebral cortex are the nervous elements of this organ and that they collectively constitute rather less than a cubic inch of protoplasm, it seems almost incredible that they should serve us as they do. They are the materials whose activities represent all human mental states, sensations, memories, volitions, emotions, affections, the highest flights of poetry, the most profound thoughts of philosophy, the most far-reaching theories of science, and, when their action goes astray, the ravings of insanity. It is this small amount of protoplasm in each of us that our whole educational system is concerned with training and that serves us through a lifetime in the growth of personality."

7. Craniospinal Nervous Pathways

Of the different bundles of fibers connecting brain and spinal cord, four groups were mentioned in the discussion of the cord. Three of these were the dorsal columns (*fasciculi gracilis* and *cuneatus*), the spinothalamic tracts, and the spinocerebellar tracts, all of which are made up of ascending fibers; the fourth was the descending corticospinal group. We are now in a position to consider some of the cranial portions of these pathways.

(a) *Fasciculi gracilis* and *cuneatus*.—As mentioned during the discussion of the spinal cord, sensory neurons with their cell bodies in the dorsal ganglia send their neurites into the dorsal funiculus. Many of these neurites continue forward as the *fasciculus gracilis*, in the case of sensory neurons from posterior parts of the body, or the *fasciculus cuneatus*, for anterior sensory neurons. These bundles extend into the medulla as the *funiculi gracilis* and *cuneatus*, respectively. Here the neurites terminate, synapsing with the short dendrites of relaying neurons, or *sensory neurons of the second order*, which carry the impulses to more anterior parts of the brain (Fig. 642).

The neurons of the second order for the *fasciculus gracilis* have their cell bodies in the *nucleus gracilis* which lies near the region where the roof plate is broadening to form the thin velum (Fig. 633). The *nucleus cuneatus*, for the relaying neurons of the cuneate tract, is just lateral to the gracile nucleus. Most of the neurites of these relaying neurons swing in an arc ventrally to decussate (cross to the other side of the medulla), beneath the central canal and posterior part of the fourth ventricle, thus forming what is known as the *sensory decussation*. As soon as they cross the mid-line they turn sharply to run anteriorly, as the *median lemniscus* which lies near the mid-line.

* *Evolution of Man*, p. 94, Yale University Press.

In the thalamus the fibers of the second order terminate and synapse with *sensory neurons of the third order* which have their cell bodies in one of the thalamic nuclei. The neurites of these third neurons go to the *somesthetic area* of the cerebral cortex.

These tracts form pathways for sensations of touch and pressure as well as for proprioceptive impulses from the muscles, joints, and tendons.

(b) **Spinothalamic Tracts.**—

In the case of the spinothalamic tracts the sensory neurons (neurons I) synapse with neurons II within the dorsal gray matter of the cord. The neurites of these neurons of the second order cross, through the *ventral commissure*, into the spinothalamic tracts of the other side of the cord (Fig. 643). The fibers of each of these tracts reach the *thalamus*, where they synapse with the neurons of the third order which have their cell bodies in one of the *thalamic nuclei*. From this nucleus, the neurites extend to the *somesthetic area* of the cerebral cortex.

It will be recalled that physiologically the two tracts of this group are not the same. The *ventral spinothalamic tract* is a pathway for sensations of touch and pressure, the *lateral spinothalamic tract* for pain and temperature. Also the neurites of the primary sensory neurons associated with each of these tracts take somewhat different courses. The neurites carrying touch and pressure impulses run in the dorsal columns before sending collaterals into the dorsal gray horn. The neurites carrying pain and temperature impulses go directly into the gray matter at the level of entrance into the cord.

(c) **Spinocerebellar Tracts.**—The spinocerebellar tracts are important proprioceptive pathways to the cerebellum, the chief center of correlation of

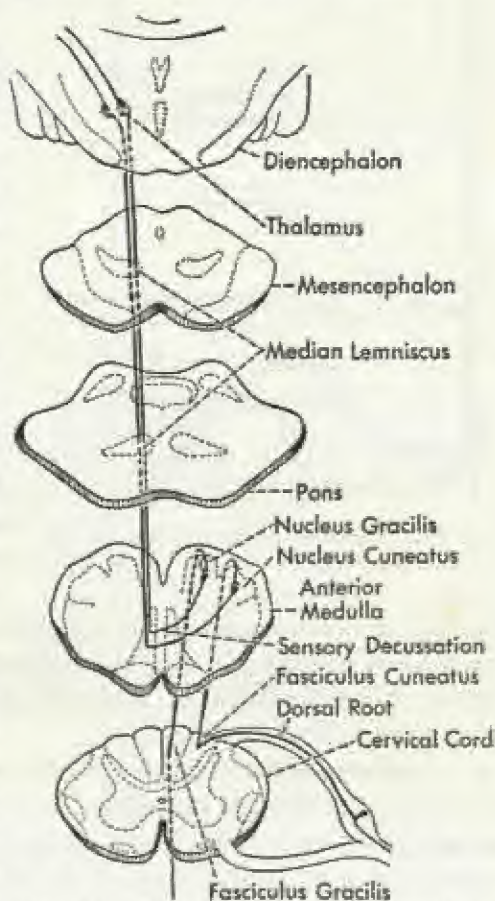


Fig. 642. Sensory pathways through the dorsal column.

these impulses as well as of coördination of muscular activity. In both of these tracts the primary sensory neurons are similar to those described for the fasciculi gracilis and cuneatus. Collaterals, leaving these neurons along

their course, enter the dorsal gray matter to synapse with the neurons of the second order.

The cell bodies of the *dorsal spinocerebellar tract* are located in the *nucleus dorsalis* (Clarke's column) from which neurites run into the dorsal tract of the same side of the cord (Fig. 616). These fibers run forward through the medulla and enter the cerebellum by way of the *restiform body* (Fig. 644).

The *ventral spinocerebellar tracts* are composed of neurites whose cell bodies are in the *dorsal horns* and adjacent portions of the gray matter. Some fibers enter the nearby tract of the same side of the cord; others cross over, through the *ventral commissure*, to run forward

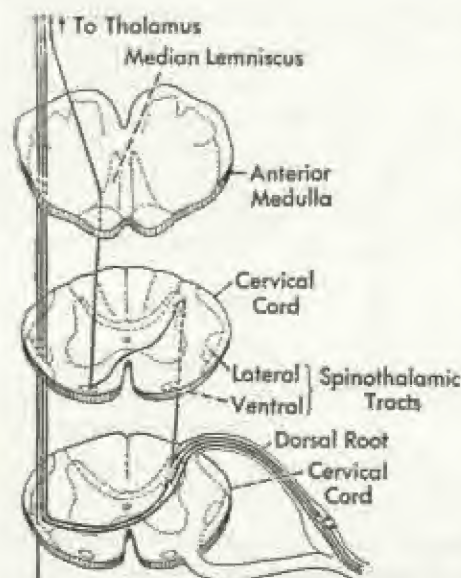


Fig. 643. Sensory pathways through the spinothalamic tracts.

through the ventral tract of the opposite side. Each ventral spinocerebellar tract passes through the *medulla* and deeper part of the *pons* to enter the *anterior cerebellar peduncle*, through which it swings back into the anterior part of the cerebellum (Fig. 645).

(d) **Corticospinal Tracts.**—Numerous motor pathways eventually leave the spinal cord through the primary motor neuron or "final common path," as mentioned previously. Many groups of fibers exert involuntary control over the muscles, while several which descend from the cerebral cortex place the skeletal muscles under voluntary control. The most important voluntary tracts entering the spinal cord are the corticospinals which originate in giant pyramidal cells of the motor cortex, immediately anterior to the central sulcus.

The neurites of these pyramidal cells pass successively through the white matter of the cerebral hemisphere, the *crura cerebri* and the *deeper part of the pons* to enter the *pyramids* of the medulla oblongata (Fig. 646). In the *pyramidal decussation*, at the posterior end of the medulla, most of these fibers cross over to become the *lateral pyramidal*, or *lateral corticospinal*,

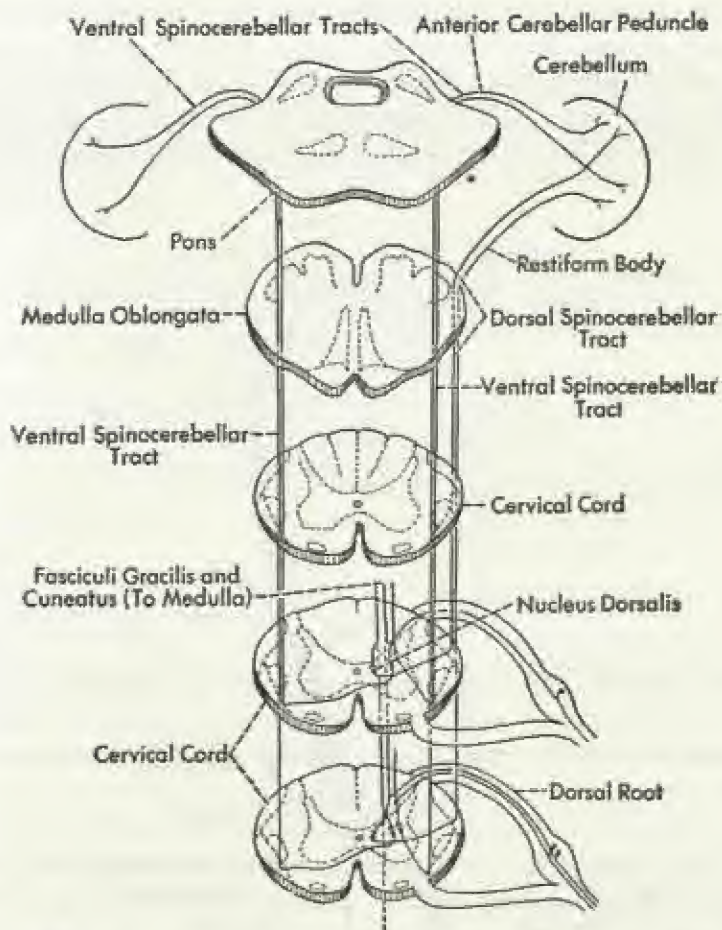


Fig. 644. Sensory pathways through the spinocerebellar tracts.

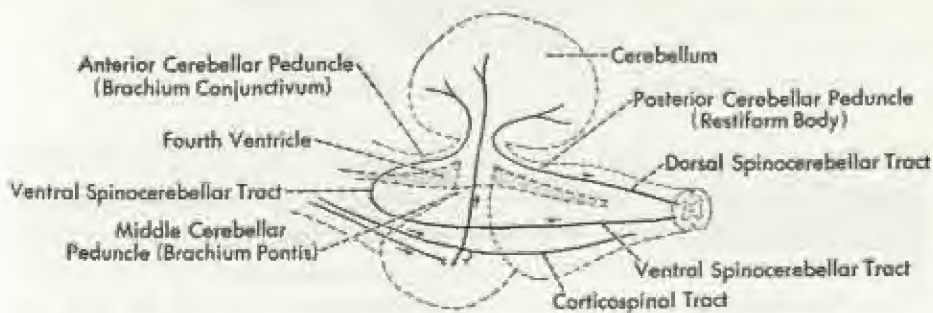


Fig. 645. The three cerebellar peduncles. (After Herrick.)

tract which continues the entire length of the cord (Fig. 619). At every segment some of these fibers enter the ventral horn of the gray matter to synapse with primary motor neurons. In man, about one-fourth of the fibers do not decussate but continue posteriorly as the *ventral pyramidal tract*, which ordinarily does not extend below the mid-thoracic region. When these

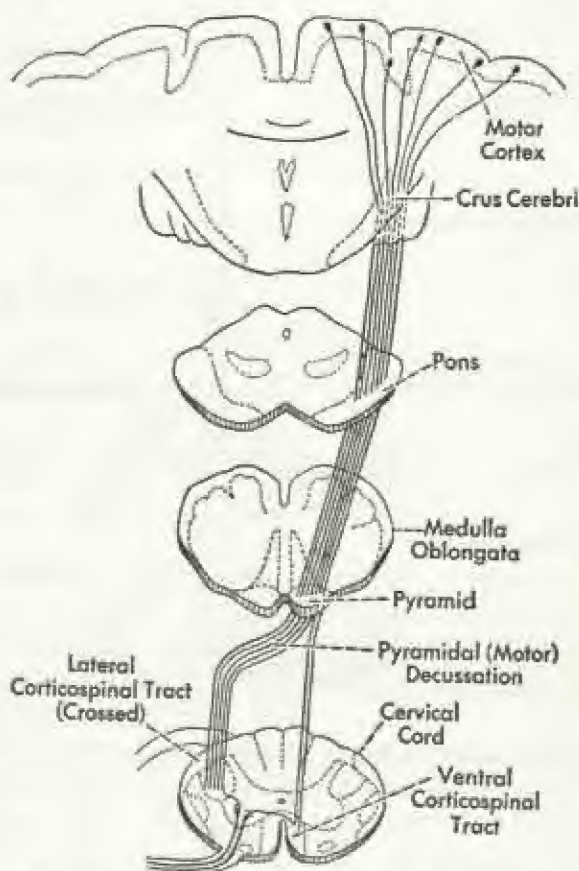


Fig. 646. The corticospinal (motor) pathways.

direct fibers leave the tract, a few at a time, they cross to the other side of the cord and enter the ventral gray horn where they synapse with the primary motor neurons. Thus while in one case the fibers cross in the medulla, in the other they cross near their termination in the cord; but all of them cross. Consequently all of the skeletal muscles of one side of the body are under the voluntary control of the motor cortex of the opposite side of the brain.

8. The Comparative Anatomy of the Brain

The essential features of the comparative anatomy of the vertebrate brain may be passed in review by an examination of diagrams of the brain of various vertebrate types (Figs. 647-652) which may be compared also with the diagram of a vertebrate brain based principally upon that of a cyclostome (Fig. 630).

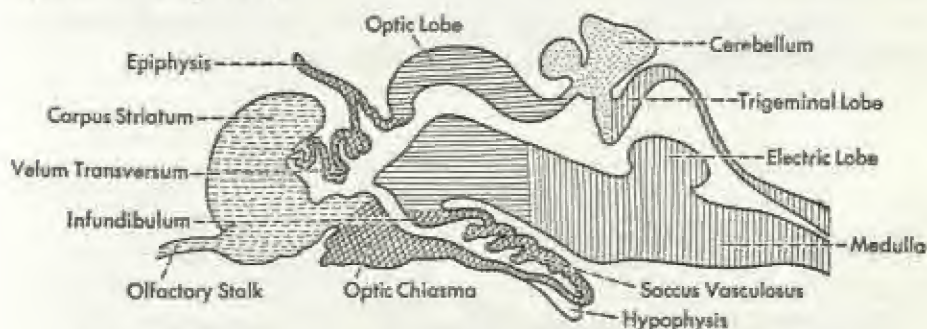


Fig. 647. Sagittal section diagram of the brain of the electric ray, *Torpedo*. (After Edinger.)

(a) *Cyclostomes*.—The brain of the lamprey eel, *Petromyzon*, is without marked flexures and quite primitive in plan. Connected with the relatively large medulla are six pairs of cranial nerves (V-X, inclusive), there being only ten pairs in these animals, as in fishes and amphibians. The roof of the *fourth ventricle* has an extensive vascular network.

The metencephalon of *Petromyzon* includes a rudimentary lip-like *cerebellum* but no *pons*, while both are lacking in *Myxine*. The roof of the mesencephalon has but one pair of swellings, the *optic lobes*. As the wall of

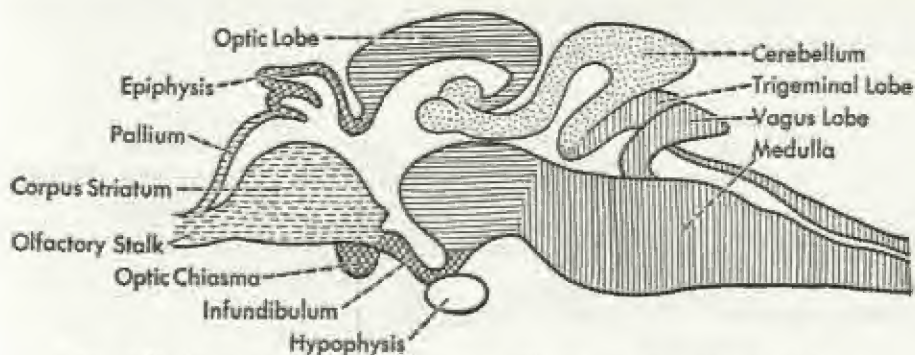


Fig. 648. Sagittal section diagram of the brain of a teleost (After Edinger.)

this region remains relatively thin there are large *optic ventricles* which are not separated from the aqueduct.

The *infundibular region* and the *thalamus proper* are small. The *epithalamus* includes a pair of *habenular ganglia* connected by a *commissure* as in all vertebrates. There are two outgrowths from the habenular region: a well developed *epiphysis* (*pineal organ*), anterior to which is a smaller *parietal body*. These two organs, arising from a common origin, were probably originally paired, since the pineal body is in intimate relation with the right habenular ganglion, and the parietal body with the left.

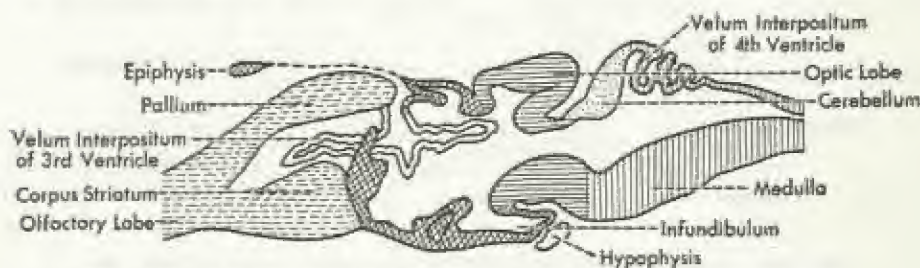


Fig. 649. Sagittal section diagram of the brain of an amphibian. (After Edinger.)

The presence in certain fossil fishes, for example *Titanichthys*, of a pair of foramina located side by side in the skull directly above this region in the brain, also seems to point to the originally paired relation of these organs. Apparently the tandem-like position of the pineal and parietal bodies in cyclostomes is the result of a secondary displacement of the former side-by-side arrangement.

The histological structure of the epiphysis, or pineal body, as well as its access to light through a foramen in the dorsal region of the skull, seems to indicate that it is, in cyclostomes at least, a photoreceptive organ by means of which light and darkness are distinguished.

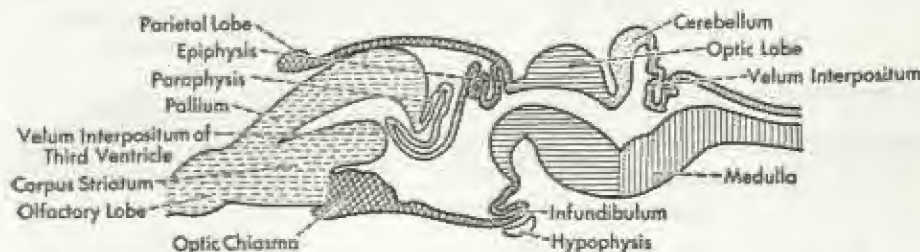


Fig. 650. Sagittal section diagram of the brain of a reptile. (After Edinger.)

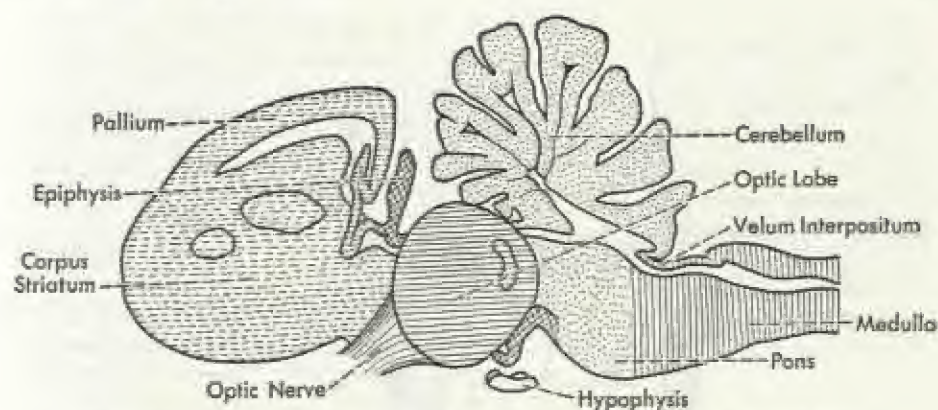


Fig. 651. Sagittal section diagram of the brain of a bird. (After Edinger.)

The rather small telencephalon, olfactory in function, includes paired *olfactory bulbs*, *olfactory lobes*, and weakly differentiated *corpora striata*. An *anterior commissure*, found in all vertebrates, connects the two sides of the brain in the region of the *lamina terminalis*.

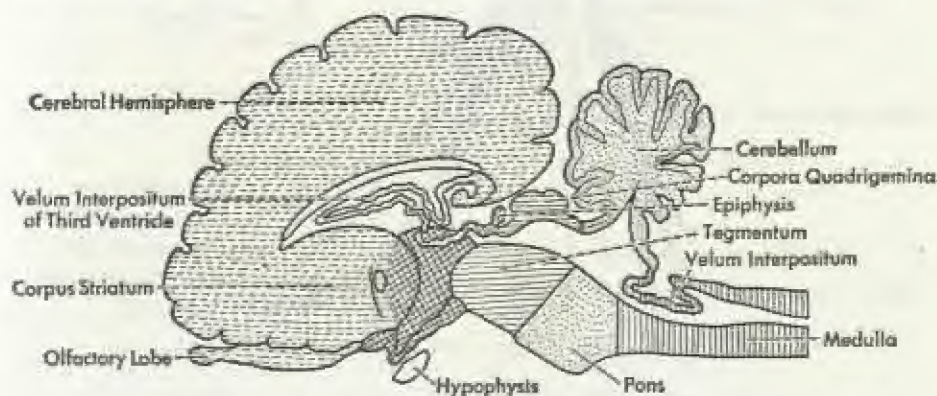


Fig. 652. Sagittal section diagram of the brain of a mammal. (After Edinger.)

(b) **Elasmobranchs.**—In elasmobranchs the bulging *corpora striata*, which even grow into the *lamina terminalis*, and the dominant *olfactory lobes* constitute the bulk of the telencephalon (Figs. 647 and 653). From each olfactory lobe there extends forward a conspicuous *olfactory stalk*, terminating in an *olfactory bulb* which may be quite large. The *velum interpositum*, the thin roof of the third ventricle, develops an invaginated transverse fold, or *velum transversum*, which marks the posterior limit of the dorsal part of the telencephalon.

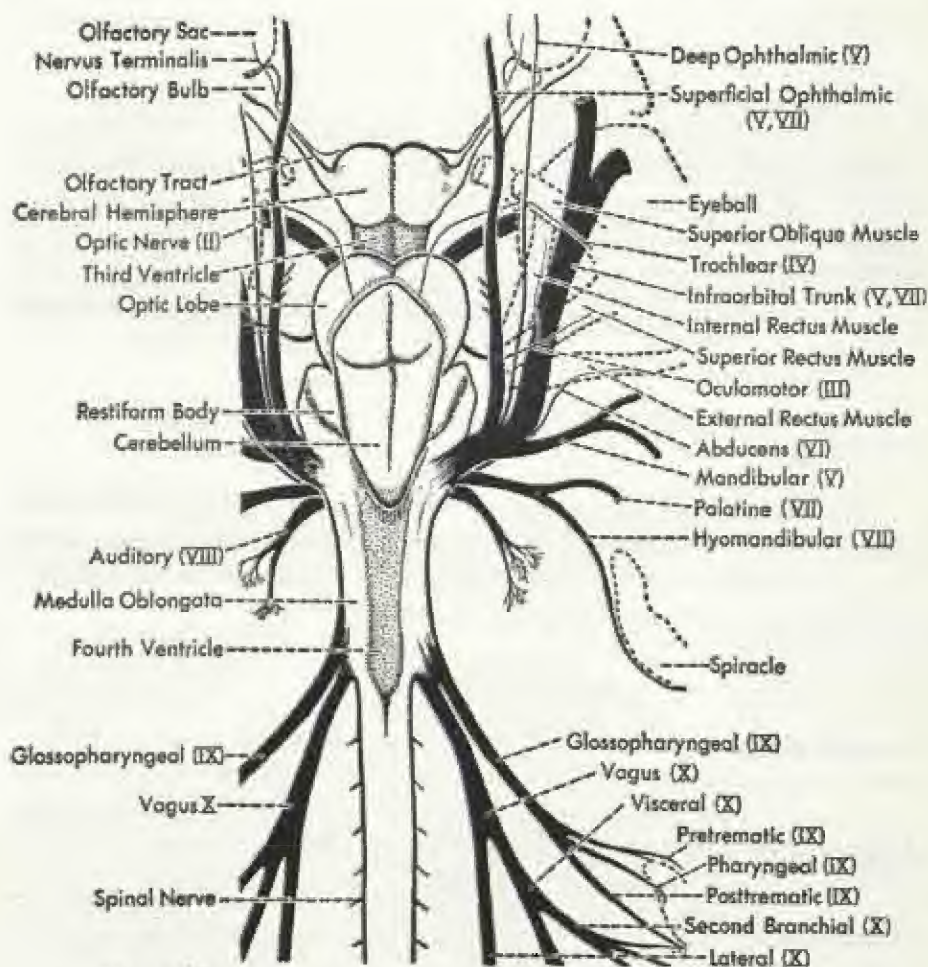


Fig. 653. Dorsal view of the brain of an elasmobranch, *Squalus*.

In the diencephalon the *epiphysis* is stalked, reaching as far as the cartilaginous roof of the cranium in many cases. The parietal organ disappears after temporary appearance during embryonic development. The *infundibulum* develops a pair of elongate swellings, the *inferior lobes*, between which the hypophysis is attached. Posterior to the inferior lobes and dorsal to the neuro-hypophysis proper, is a thin-walled *vascular sac*, or *saccus vasculosus*, lined with a sensory epithelium of problematical significance. This sac is not found in cyclostomes or tetrapods.

The well developed *optic lobes* may be partially covered by a large *cerebellum*. As would be expected, the cerebellum is much larger in the active dogfishes and sharks than in the sluggish skates and rays.

In the antero-lateral part of the medulla, connecting it with the cerebellum, are prominent *restiform bodies* which stand out like a pair of ears on either side of the cerebellum. In elasmobranchs, as in embryonic stages of higher vertebrates, the differentiation of the medulla into four longitudinal areas is clearly visible. These four columns represent the same four nervous components described for the cord. On either side of the thin ependymal velum which forms the roof of the fourth ventricle are the *somatic sensory columns* ventral to which are the *visceral sensory columns*, then the *visceral motor columns*, and finally the *somatic motor columns* which lie on either side of the median plane in the floor of the ventricle (Fig. 654).

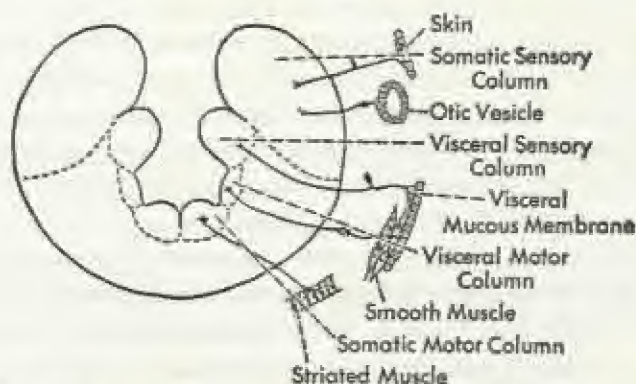


Fig. 654. Diagrammatic cross section through the medulla of an elasmobranch to show the four areas and the parts they supply. (After Johnston.)

The electric *Torpedo* has two *electric lobes* (Fig. 647) that project into the fourth ventricle. These structures are hypertrophied nuclei of the vagus (X) nerve which supplies the electric organ of these animals.

(c) **Other Fishes.**—In bony fishes the brains are small and show great variations. The roof of the telencephalon is thin and non-nervous (Fig. 648). Convex corpora striata occupy the floor of this region. The shortened epiphysis is on the downward road of degeneration. The optic lobes are large, especially in teleosts. The cerebellum, small in dipnoans and ganoids, is large in most teleosts, especially the most active ones.

(d) **Amphibians.**—In amphibians (Fig. 649), the large elongated *olfactory lobes*, which are continuous with the distinctly separated *cerebral lobes*, lie closely side by side and are joined medially together.

The *corpora striata* project upward from the telencephalic floor only slightly, allowing for fairly large *lateral ventricles* and invaginated anterior

choroid plexuses inside the cerebral lobes. The latter are without an external layer of gray matter, although scattered neurons begin to appear in the thickening pallial wall.

The diencephalon is uncrowded, and visible from above, without inferior lobes or saccus vasculosus. In adult anurans the *epiphysis* is represented by a small median vesicle, the pineal gland, close under the dorsal wall of the cranium, which by its development is shown to be the bulbous tip of the vanished stalk of the epiphysis. Skulls of stegocephals have a dorsal foramen, which shows the presence in those primitive amphibians of either a pineal or a parietal eye in this region. The parietal body is absent in modern amphibians.

The optic lobes have been so spread apart as to occupy a more lateral position, and the cerebellum, reduced to a transverse lip in most forms, is quite rudimentary in the caecilians as well as in some urodeles.

(*c*) **Reptiles.**—The reptilian brain (Fig. 650) shows an advance in the telencephalic region, since a gray cortex, although not pronounced, is definitely laid down, and the commissures between the cerebral lobes are somewhat more developed than in the amphibian brain.

The corpora striata are so large that only small lateral ventricles remain. In most reptiles the olfactory lobes are hardly distinguishable from the neopallial part of the telencephalon, but in those lizards and alligators with prominent projecting snouts the olfactory lobes are extended into stalks and bulbs, as in elasmobranchs.

The diencephalic region of the brain of reptiles is of particular interest. The thalami are large, while the hypophysis attached to the infundibulum is definitely differentiated into an anterior and a posterior part, the former enveloping the latter. On the thin dorsal wall of the third ventricle there are, at least embryonically, not only pineal and parietal outgrowths, but also a third evagination, the *paraphysis* (Fig. 418), which is so far anterior in position that it actually belongs to the telencephalon. The paraphysis usually undergoes degeneration in adult life and its function is still unknown.

Except in crocodiles and alligators, the epiphysis is always present as a glandular pineal structure. The parietal organ is also always present in close association with the same habenular centers as those of the pineal body. Reaching its highest development in *Sphenodon*, in which it extends as far as a transparent window on the roof of the skull, it is unmistakably a third median eye, equipped with a retina and a lens.

In snakes distinct corpora quadrigemina occur in the dorsal part of the mesencephalon. It has been shown, however, that other reptiles and possibly amphibians have small auditory centers, corresponding to posterior colliculi.

These auditory centers do not show as a pair of elevations until the optic centers become reduced to anterior colliculi occupying only the anterior part of the roof of the mesencephalon. The thickening of the mesencephalic wall reduces the cavity of this region to a slender canal, the aqueduct.

The cerebellum of reptiles is usually small, although fairly well developed in swimming forms. Eight pairs of cranial nerves (V–XII inclusive) connect with the medulla as in birds and mammals, whereas only six pairs (V–X inclusive) occur here in anamniotes.

(f) **Birds.**—The brain of birds (Fig. 651) is more of an "eye brain" than a "nose brain," thus showing an advance over its forerunners. The cerebral cortex, however, is less well developed than in reptiles, with the corpora striata more in evidence. The lateral ventricles, due to the increased thickness of the corpora striata, are reduced to very restricted spaces.

The olfactory lobes were fairly prominent in the tooth-bearing cretaceous birds, but are small and degenerate in their modern representatives. No trace of a parietal organ appears in birds, and since the degenerate pineal body is buried between the encroaching cerebrum and cerebellum, the entire brain gives the impression of compact crowding and centralization, characteristic of the bird's structure generally. This is due not only to the fact that the greatly enlarged optic lobes are crowded over laterally in position, but also to a considerable backward growth of the cerebrum which tends to bury the diencephalon and the mesencephalon from dorsal view.

The cerebellum, consisting of a well-defined median *vermis* as well as two *lateral lobes*, is very large, as might be expected in these extremely active animals.

(g) **Mammals.**—Tertiary mammals, as methods of exploring the cranial cavity of fossil skulls reveal, had a reptilian type of brain. In modern mammals also, the brain (Fig. 652) is more like that of reptiles than that of birds, since the outstanding size of the cerebrum is due to the development of the cortex rather than to an enlargement of the corpora striata, as is the case among birds.

The commissural systems between the cerebral lobes are better developed than in other vertebrates, particularly by the elaboration of the large corpus callosum, although this is small in the monotremes and marsupials.

While still prominent in the monotremes, marsupials, and other lower mammals, the archipallial olfactory part of the brain becomes reduced among the higher mammals, until in man it is very small, and in seals and whales almost entirely lacking.

In the diencephalon the thalami are large. The epiphysis, now connected with endocrine activity and having lost its eyelike structure, is reduced to

an organ degenerate in size, although indispensable in function. It is usually covered over by the hemispheres and is relatively large in ungulates and rodents but missing in armadillos and other edentates.

The two optic lobes of lower forms become changed in mammals into four corpora quadrigemina, which are relatively smaller than is this region of the mesencephalon in any other vertebrate. The corpora quadrigemina are quite covered by the overgrowth of the massive cerebrum and the cerebellum which have so enlarged that they meet dorsally.

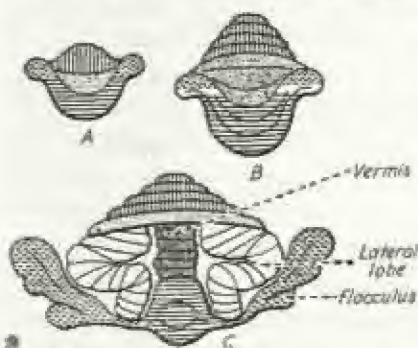


Fig. 655. Evolution of the cerebellum. A, crocodile; B, bird; C, mammal. Anterior lobe, vertical lines; median lobe, dots; posterior lobe, horizontal lines. (After Ransom and Inguar.)

In addition to enlarged vermis and lateral lobes, *flocculi* of considerable size are present (Fig. 655). Thus the correlation tissue of the cerebellum is notably increased.

A further characteristic of the mammalian brain is a definite band of fibers encircling the brain stem, known as the *pons*, in the metencephalic region. The

medulla of mammals is comparatively short, and appears to be drawn under the prominent cerebellum.

9. The Control of the Body by the Brain

Animal activities having their physical basis in the brain are of three general categories, namely, (1) *innate stereotyped functions*, which are inherited, and are ordinarily blanketed together under the term *instinct*; (2) *habits*, which are not inherited but are patterns of conduct acquired by repetition until they become more or less automatic; and (3) *variable modifiable actions*, which are marks of intelligence that are perfected by the process of learning.

Innate stereotyped functions, it may be said, do not lend themselves to individual improvement. It is futile, for example, to try to teach a grasshopper either to jump or to dance. It jumps already, having been born an instinctive jumper, and it can never learn to dance, since the "variable, modifiable" capacity is practically wanting in its make-up.

With an increase of cerebral function the instinctive automatic reflexes take more and more to the background, and therein is the great distinction between "lower animals," that are largely at the mercy of their environment and heredity, and the "higher animals," which to an increasing degree

have risen above environing conditions and their hereditary handicaps, and have become more and more "captains of their souls." One of the most prized possessions of mankind is the "capacity for individuality," yet even what passes for "free will" has its basis in the neurons and reflexes built up in the brain. In the last analysis the brain must be regarded as the mechanism through which consciousness, memory, imagination, and will are effected.

The control which the brain, and particularly the cerebral cortex, exercises over the body is increasingly greater as one passes from fishes to mammals. A "spinal frog," in which the brain has been destroyed but the spinal cord left intact, continues to perform many of its functions in an apparently normal fashion. A hen with its head cut off continues to flop about for some time, but not so a mammal that has been guillotined. In man a comparatively slight interference with even a minute portion of the cortex may result in sudden fatal apoplexy.

An important function of the brain and the cord that should be mentioned is their activity as *inhibitors* of many of the myriad reflexes called forth continuously by an insistent environment. Without such automatic inhibitions man would be worn out by continuous responses to a great variety of stimuli to which he is constantly exposed. Relief from incessant activity is gained not only by the inhibitory action of the nervous system, but also by periods of unconsciousness during sleep. It has been estimated that a person seventy years of age has lost consciousness over 25,000 times in sleep.

X. CRANIAL NERVES

Cranial nerves are more specialized than spinal nerves, since they have more differentiated tasks to perform, yet they bear an unmistakable family resemblance to their spinal relatives.

In some respects the cranial nerves may represent the ancestral type, as exhibited by all of the segmental nerves of amphioxus and the lamprey eels. It will be recalled that in these lower chordates the dorsal and ventral roots of all nerves remain separate and that the dorsal roots include visceral motor fibers which supply the internal organs. In all vertebrates the cranial nerve roots also remain separate, some cranial nerves (III, IV, VI, and in amniotes XII) representing the motor ventral roots, while others (V, VII, IX and X) are mixed dorsal root nerves which include not only sensory fibers but also visceral motor components. Two other cranial nerves are also dorsal-root nerves but are not mixed, the auditory (VIII) including only

sensory fibers while the spinal accessory (XI) of amniotes is made up solely of visceral motor elements. The olfactory (I) and optic (II) "nerves" belong to entirely different categories from the others as will be shown when they are specifically considered.

Some factors that have influenced the modifications of the cranial nerves are as follows: (1) the presence of sense organs located in the head; (2) the elaboration in water-dwelling vertebrates of the splanchnocranium; and (3) the degeneration of most of the embryonic myotomes in the head region (Fig. 583).

Although the dorsal sensory roots of the spinal nerves arise solely from dorsal ganglia that have formed from the neural crest of the early embryo, some of the neurons of certain of the cranial nerves (V, VII, IX, and X) have their origin in patches of thickened ectoderm, the *epibranchial placodes*.

No two pairs of cranial nerves have the same uniform make-up. For example, in addition to the four *general* functional types of neurons characteristic of spinal nerves, namely, *somatic afferent* and *visceral afferent* neurons of the dorsal root, and *somatic efferent* and *visceral efferent* neurons of the ventral root, there are present three other types, namely, *special somatic afferent* and *special visceral afferent* neurons associated with the superimposed cranial sense organs of sight, hearing, smell, and taste; and *special visceral efferent* neurons in connection with the branchiomic meric musculature of the primitive gill arches and their derivatives.

No single pair of cranial nerves possesses all of these seven functional types of elements, and rarely do two pairs have the same composition, as will be evident from the inspection of Table XI.

It will be seen that the sensory elements of the cranial nerves (column 5), as in spinal nerves, are associated with *ganglia* located outside the brain itself. The efferent motor elements, on the other hand, have their headquarters in *nuclei* within the gray substance of the brain.

The twelve pairs of cranial nerves were first identified in man and are named with reference to the parts which they supply, being customarily designated by the Roman numerals I to XII. The first two pairs, or olfactory and optic, are in a class by themselves. The eight cranial nerves from III to X inclusive have been called "spinal-cranial nerves," because they can be interpreted as modified spinal nerves. The XIth and XIIth cranial nerves, occurring only in amniote vertebrates, show most of all the spinal character, although the hypoglossal (XII) has lost its dorsal sensory root, which was present in the embryo.

In lower vertebrates there is a group of from one to five pairs of small

TABLE XL Cranial Nerves

NUM-BER	NAME	SUPERFICIAL ORIGIN	COMPOSITION OF FUNCTIONAL COMPONENTS	POINT OF ORIGIN	TERMINAL SUPPLY
0	Nervus terminalis	Telencephalon	General somatic afferent	Cerebral hemispheres	Nasal septum
I	Olfactory	Rhinencephalon	Special visceral afferent	Olfactory mucous membrane	Olfactory bulb and lobe
II	Optic	Diencephalon	Special somatic afferent	Retina	Lateral geniculate body: pulvinar: superior colliculus
III	Oculomotor	Mesencephalon	Somatic efferent	Oculomotor nucleus	Extrinsic eye muscles (except superior oblique and lateral rectus)
			General visceral efferent General somatic afferent	Edinger-Westphal nucleus	Ciliary ganglion and intrinsic eye muscles Proprioceptive from eye muscles (except as above)
IV	Trochlear	Anterior medullary velum	Somatic efferent General somatic afferent	Trochlear nucleus	Superior oblique muscle Proprioceptive from superior oblique muscle
V	Trigeminal	Myelencephalon	General somatic afferent Special visceral efferent General somatic afferent	Gasserian ganglion Motor nucleus of V	Skin and stomodaeal epithelium Motor fibers to muscles of mastication Proprioceptive from muscles of mastication

TABLE XL Cranial Nerves (*Continued*)

NUMBER	NAME	SUPERFICIAL ORIGIN	COMPOSITION OF FUNCTIONAL COMPONENTS	POINT OF ORIGIN	TERMINAL SUPPLY
VI	Abducens	Myelencephalon	Somatic efferent General somatic afferent	Abducens nucleus	Lateral rectus muscle Proprioceptive from lateral rectus muscle
VII	Facial	Myelencephalon	Special visceral afferent General visceral efferent Special visceral efferent	Geniculate ganglion Superior salivatory nucleus Motor nucleus of VII	Taste-buds in anterior two-thirds of tongue Submaxillary and sublingual salivary glands Superficial face and scalp muscles, platysma, posterior belly of digastric, stylohyoid muscle
VIII	Acoustic	Myelencephalon	Special somatic afferent Proprioceptive	Spiral ganglion Vestibular ganglion	Organ of Corti Semicircular canals, utricle, sacculus
IX	Glossopharyngeal	Myelencephalon	General visceral afferent Special visceral afferent General visceral efferent Special visceral efferent	Petrosal ganglion Petrosal ganglion Inferior salivatory nucleus Nucleus ambiguus	Pharynx and posterior third of tongue Taste buds in posterior third of tongue Parotid gland Muscles of pharynx

X	Vagus	Myelencephalon	General somatic afferent General visceral afferent Special visceral afferent General visceral efferent Special visceral efferent	Jugular ganglion Nodosal ganglion Dorsal motor nucleus of X Nucleus ambiguus	External ear Pharynx, larynx, trachea, esophagus, thoracic and abdominal viscera Taste buds of epiglottis Thoracic and abdominal viscera via sympathetic ganglia Striated muscles of pharynx and larynx
XI	Spinal accessory	Myelencephalon	General visceral efferent Special visceral efferent Special visceral efferent	Dorsal motor nucleus of X A. Nucleus ambiguus B. Anterior gray column of cord	Thoracic and abdominal viscera via sympathetic ganglia Striated muscles of pharynx and larynx Trapezius and sternocleidomastoid muscles
XII	Hypoglossal	Myelencephalon	Somatic efferent	Hypoglossal nucleus	Musculature of tongue

transitional *spino-occipital* nerves in the region where the medulla passes over into the spinal cord. Although entirely postcranial in cyclostomes, the more anterior ones become enclosed within the skull in fishes and amphibians. These nerves, which usually lack dorsal roots and are therefore purely motor, supply muscles associated with the gill region. In amniotes the persistent portions of these nerves participate in the formation of the XIth and XIIth cranial nerves which are added to the ten already present in anamniotes. The XIth arises chiefly from roots split off from the Xth nerve of lower forms but with the addition of a few twigs from the most anterior spino-occipital nerves. The hypoglossal (XII) nerve, which supplies the tongue, is the result of the fusion of several of the spino-occipital nerves the central connections of which shift forward to the medulla region.

Since the identification of the twelve classical pairs of cranial nerves, the somewhat embarrassing discovery of an additional pair has been made (Fig. 653). This extra pair, called the *nervus terminalis*, was first found in the lungfishes and is now known to be present, at least embryonically, in all classes of vertebrates including man. As the *nervus terminalis* is anterior to all the other cranial nerves, it remains without a Roman numeral, since its logical designation as the first pair would upset the well-established and generally accepted succession of the other twelve pairs. Consequently it is numbered 0.

It will be seen from Table XI (column 3) that most of the cranial nerves take their apparent origin from the myelencephalon, or medulla (Fig. 635). The exceptions are the *nervus terminalis* (0) and the olfactory (I), which connect with the telencephalon; the optic (II) from the dien-cephalon; the oculomotor (III) from the mesencephalon; and the trochlear (IV) from the intermediate region between the mesencephalon and the metencephalon.

Furthermore, as far as function is concerned, I, II, and VIII are entirely sensory in character, lacking motor roots, while XI and possibly XII, having lost their sensory components, are entirely motor. Although formerly considered to be purely motor because of the absence of typical sensory roots, III, IV, and VI are now known to be mixed for they include proprioceptive fibers. The *nervus terminalis* (0) is of doubtful function. The remaining pairs, namely, V, VII, IX, and X, are mixed nerves, although some of them have *branches* that are either entirely sensory or entirely motor in character.

With regard to neuronie components, the distribution is shown in Table XII.

A typical mixed cranial nerve, like the spinal nerves, divides into dorsal and ventral branches, distal to its ganglion. The short dorsal branch in fishes,

containing only afferent neurons, brings the sensations to the brain from the skin and the lateral-line organs. It becomes much reduced in land forms and eventually disappears entirely.

The ventral branch usually forks into a *pretrematic* twig and a *post-trematic* twig, that extend on either side of the splanchnocranial openings, such as the mouth, spiracle, and gill slits. These twigs of the ventral branch may carry either efferent or afferent neurons and in some cases both. Usually there is also a sensory *pharyngeal* twig to the pharyngeal lining.

TABLE XII. Cranial Nerve Components

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
General somatic afferent			p	p	#p	p				#		
General visceral afferent									#	#		
Somatic efferent			#	#		#						#
General visceral efferent			#				#		#	#	#	
Special somatic afferent		#						#p				
Special visceral afferent	#						#		#	#		
Special visceral efferent					#		#		#	#	#	

p, proprioceptive fibers

There is evidence that the trigeminal nerve (V) is compounded of two original nerves. The facial (VII) probably represents the dorsal root of a nerve of which the abducens (VI) corresponds to the ventral root.

The acoustic nerve (VIII), now entirely sensory and independent, was probably a part of the VIIth nerve formerly, while the vagus (X) is no doubt a complex of multiple origin concerned with several branchial arches, having the spinal accessory (XI) split off from it as an independent nerve.

Thus the homologies of the cranial nerve become a complicated problem, calling for much patient and searching investigation on the part of comparative anatomists.

The following brief survey of the separate cranial nerves supplements the information buried in Table XI.

I. Terminal Nerve (0)

The terminal nerve arises from the cerebral hemispheres in the region of the medial olfactory tract and extends to the snout region in close association with, but independent of, the olfactory nerves.

It possesses one or more ganglia and is of doubtful function, being

described as sensory by some investigators, as part of the autonomic system by others.

2. Olfactory Nerve (I)

The olfactory nerve is peculiar in that its fibers arise from cells of the olfactory epithelium. The dendrites of these cells have thickened endings which are exposed on the surface of the epithelium. The unmyelinated neurites making up the nerve have only a short distance to run to reach the olfactory bulb of the brain. In cyclostomes, which have only a single nasal sac, the olfactory nerves are paired as usual, indicating that the single organ represents a fusion of what was formerly two sacs.

In the skull of most vertebrates the olfactory nerve passes through a single foramen on either side to reach the brain, but in many of the higher animals it consists of a brushlike bundle of non-medullated fibers, *fila olfactoria*, that penetrate the skull separately through the pepperbox-like pores of the cribriform plate of the ethmoid bone. Thus, in man, instead of a single pair of olfactory nerves, it would not be entirely incorrect to say that there are at least twenty pairs.

3. Optic Nerve (II)

The optic nerve is not a true nerve but rather a *tract* of the brain both in development and structure. In development an evagination from the diencephalon forms the retinal layer of the eyeball (Fig. 706). Then some of the retinal cells send their neurites back to the brain as the optic nerve, which therefore connects two parts derived from the embryonic central nervous system, the retina and the diencephalon. The fibers which make up this nerve, like most fibers in nerve tracts, are myelinated but without any neurolemma.

Upon reaching the ventral side of the diencephalon the fibers decussate, in the optic chiasma, before passing into the brain. The crossing of the fibers is complete except in the higher mammals in which the fibers from the nasal half of the eyeball cross while those from the temporal half do not. In man, therefore, the fibers from the left halves of the two eyes go to the left side of the brain, those from the right halves to the right side of the brain (Fig. 656). This arrangement develops in association with improvement in binocular vision. After passing through the chiasma region, the fibers continue as the *optic tracts* each of which, after running over the outer surface of a cerebral peduncle, sends fibers into three parts of the brain, the *lateral geniculate body*, the *anterior colliculus*, and the region just anterior to the latter (Fig. 633).

In these three pairs of regions the fibers of the optic tract synapse with neurons which relay the impulses to several different parts of the brain. From the lateral geniculate bodies the relaying fibers run chiefly to areas of visual sensation in the occipital cerebral cortex (Fig. 640). The anterior colliculi, which receive fibers from the occipital cortex as well as the optic tracts, relay messages to the nuclei of the several cranial nerves which control the movements of the eyeballs and also of the head. Fibers from the area just in front of each anterior colliculus carry impulses which eventually reach the intrinsic muscles of the eyeball.

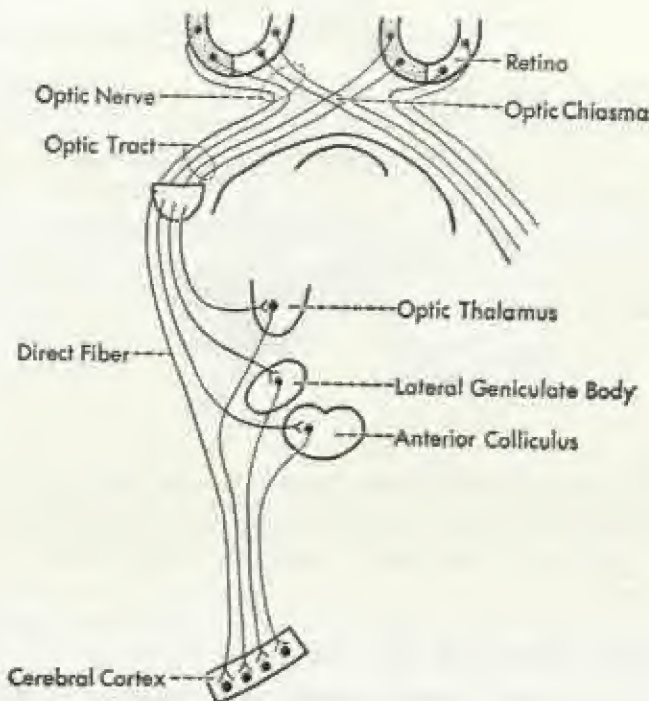


Fig. 656. Optic chiasma and tracts of man.

The intricate optic pathways of mammals have evolved from a relatively simple plan in lower vertebrates. In fishes most of the optic-tract fibers run into the optic lobes (Fig. 657). In reptiles optic lobes continue to be highly important relaying centers in the optic pathways, but some optic fibers terminate in the diencephalon where they synapse with neurons leading to the cerebral cortex, which is definitely present in these animals. In mammals relatively few primary optic fibers go to the metencephalon, most of them terminating in the lateral geniculate bodies of the diencephalon.

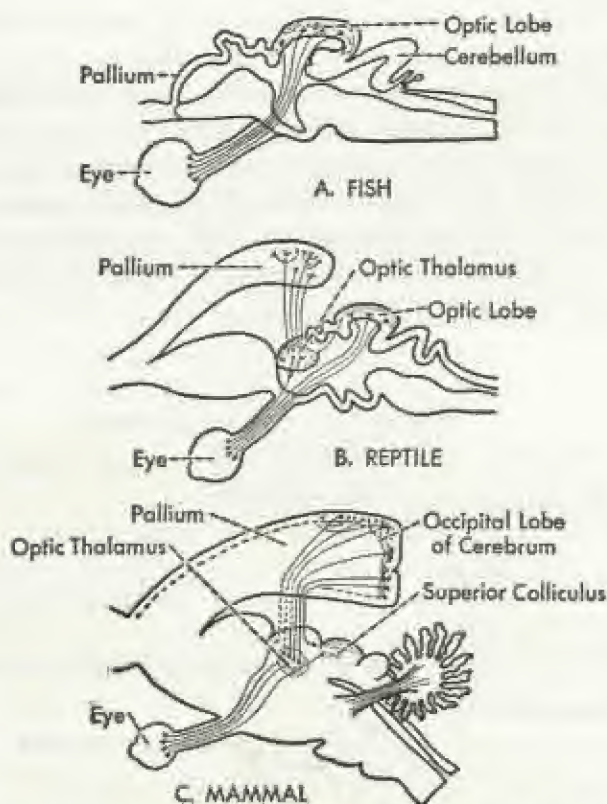


Fig. 657. Evolution of the optic tracts. A, fish; B, reptile; C, mammal. The dorsal part of the mesencephalon, which is the primitive visual center, becomes a relay center in mammals. In the latter group the definitive visual centers are in the occipital lobes of the cerebrum. (After Monakow.)

4. Eye-Muscle Nerves (III, IV, VI)

The nerves of the eyeball muscles have much in common, being efferent somatic nerves associated with the three pairs of myotomes that remain in the head region (Fig. 583). The oculomotor (III) and the trochlear (IV) arise from the mesencephalon, while the abducens (VI) comes from the myelencephalon. No cranial nerves take their origin from the metencephalon.

The most important nerve of the eye muscles is the *oculomotor*, which supplies not only the *inferior oblique* and three of the *rectus* muscles, namely, *superior*, *inferior*, and *internal*, but also the *levator palpebrae* that lifts the upper eyelid, as well as the intrinsic *iris* and *ciliary* muscles of accommodation within the eyeball itself.

The *trochlear* supplies the *superior oblique* muscle. The two trochlears decussate in the anterior medullary velum.

The *abducens* actuates the *lateral*, or *external*, *rectus* muscle. It also sends a branch to the *retractor bulbi*, a muscle derived from the external rectus, which pulls back the eyeball as the name implies. This muscle is present in all tetrapods except ophidians and primates. The *nictitating membrane*, or third eyelid of reptiles, birds, and some mammals, is also supplied by the abducens nerve.

All three of these nerves are now believed to include proprioceptive sensory fibers from the structures which they supply.

5. Trigeminal Nerve (V)

The *trigeminal nerve* comes off dorso-laterally from the anterior region of the medulla in close association with the VIIth and the VIIIth cranial nerves, constituting together a most important group for the supply of the head. It has a strong dorsal root and a lesser ventral root and is one of the largest of the cranial nerves. It is the great sensory nerve of the head carrying nearly all of the general somatic sensory fibers from the surface of the head to the brain. The cell bodies of these fibers are located in the *Gasserian ganglion* of the dorsal root, one of the largest of all the ganglia associated with cranial nerves.

The trigeminal nerve is so called because of its three component branches, the *ophthalmic*, *maxillary*, and *mandibular*. It was probably formed by the joining of two original dorsal root nerves, the ophthalmic being the remains of one, and the maxillary and mandibular of the other. According to this interpretation the corresponding ventral root nerves are the oculomotor and the trochlear.

In fishes the *ophthalmic*, which is sensory in all animals, supplies the skin of the snout and dorsal part of the head. In mammals it is distributed to the nose, orbit, forehead, and top of the head. The *maxillary*, which is also sensory, goes to the teeth of the upper jaw, the upper lips, and the cheeks. The *mandibular* is mixed, being composed of: (1) sensory fibers from the teeth and skin of the lower jaw and also the skin of the side of the head; and (2) motor fibers which innervate the mandibular group of branchiomic muscles (see Chapter XVIII).

The mandibular branch also includes proprioceptive sensory fibers coming from the muscles of mastication which it supplies. These proprioceptive neurons have their cell bodies in the *mesencephalic nucleus* of this nerve. In this respect they are unique, for the sensory neurons of all other vertebrate nerves have their cell bodies in ganglia, outside of the central nervous system.

It will be recalled, however, that amphioxus has no ganglia, all of the cell bodies being within the central nervous system.

The maxillary branch may be regarded as the *pretrematic* nerve anterior to the mouth, and the mandibular branch, the corresponding *posttrematic* nerve posterior to the mouth. This pre- and posttrematic arrangement on either side of a pharyngeal opening, like mouth, spiracle, or gill slit, is repeated in other cranial nerves.

6. Facial Nerve (VII)

The VIIth nerve, or *facialis*, undergoes much modification as the result of evolutionary emergence from water to land life, owing to the loss of the lateral-line organs and, in higher mammals, to the development of the mimetic musculature of the face. The cell bodies of its sensory fibers are in the *geniculate ganglion* which in the lower vertebrates is often fused with the Gasserian ganglion of the Vth nerve.

In fishes and urodeles several dorsal branches of this nerve serve chiefly as sensory pathways from the lateral-line organs. These branches are lacking in anurans and higher vertebrates.

The ventral branch of the VIIth nerve forks into two trunks in fishes, the *palatine* and *hyomandibular*, which are respectively the pretrematic and posttrematic nerves of the spiracular opening.

In mammals the pretrematic branch is probably represented by the *chorda tympani*, a small nerve which runs through the middle-ear cavity. It will be recalled that this cavity corresponds to part of the spiracular passageway of fishes. The chorda carries fibers from the taste-buds on the anterior two-thirds of the tongue. It has also been joined by autonomic fibers associated with the sublingual and submaxillary glands. The posttrematic portion becomes the group of nerves which supply the hyoid-arch group of branchiomic muscles, including the extensive muscles of facial expression in man.

7. Acoustic Nerve (VIII)

The *acoustic*, or *auditory*, nerve is a very short sensory nerve which does not emerge from the skull. It divides into two branches, the *vestibular* and *cochlear*, that go respectively to the semicircular canals and to the auditory mechanism (cochlea) of the internal ear. Each branch has a *ganglion* of similar name. As the semicircular canals aid in maintaining equilibrium, some of the fibers of the vestibular nerve run directly to the cerebellum, the main equilibrium center of the brain. Impulses from the cochlea, like those from the eye, are distributed through various parts of the brain. After

being carried to the restiform body they are relayed to: (1) the auditory center in the cortex of the temporal lobe of the cerebrum; (2) the posterior colliculus, a center for reflexes initiated by sound; and (3) other centers in the brain including those of the several motor nerves.

8. Glossopharyngeal Nerve (IX)

The *glossopharyngeal nerve*, primarily associated with the third splanchnocranial arch, forks around the first functional gill slits of fishes and sends a branch into the pharynx. Frequently it also has a small branch associated with the lateral-line system. Its sensory fibers have their cell-bodies located in the *petrosal ganglion*.

In mammals the sensory components are connected with the taste buds of the posterior third of the tongue, and general sense organs of this region and the neighboring portions of the pharynx. Most of its efferent fibers supply pharyngeal muscles derived from the group originally associated with the third visceral arch; a few synapse with autonomic fibers running to the parotid gland.

9. Vagus Nerve (X)

The *vagus nerve*, as the name implies, "wanders" to many parts of the body. It is apparently a composite of several segmental nerves. In fishes it splits into two main trunks, *lateral* and *visceral*. The lateral trunk, which is sensory, supplies some of the lateral-line organs of the head and extends along the side of the body as the nerve of the lateral-line canal. The visceral trunk, after giving off mixed *branchial* nerves to the remaining gill arches, continues posteriorly carrying visceral afferent and efferent fibers to the heart, the blood vessels, and the digestive tract and its derivatives as far as the posterior end of the small intestine. The cell-bodies of the visceral afferent fibers are in the *nodosal ganglion*.

In strictly land vertebrates, with the loss of the lateral line system and the gills, most of the nerves connected with these structures disappear. Motor fibers of the branchial nerves persist, however, to innervate striated muscles of the pharynx and larynx. The main visceral trunk, which runs to the internal organs, retains its importance, carrying both sensory fibers and efferent fibers which connect with the autonomic nervous system.

In cyclostomes the vagus includes many somatic sensory fibers from the skin of the posterior part of the head. In fishes and amphibians these cutaneous fibers are limited to the dorsal portion of this region, while in higher forms they are associated with the skin of the external ear.

10. Spinal Accessory Nerve (XI)

The *spinal accessory nerve*, found only in amniotes, is composed entirely of visceral efferent fibers. Part of these fibers, arising from the posterior

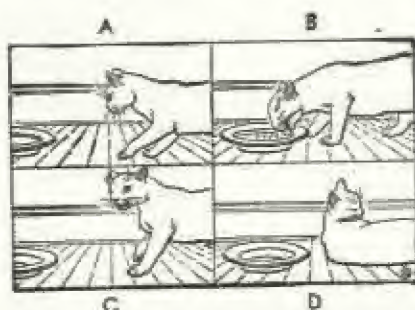


Fig. 658. The functions of the cranial nerves. A, smelling and seeing (I, II). B, smelling and seeing (I, II); convergence and accommodation (III); depression of eyeballs (III, IV); mastication (V); salivation and tasting (VII, IX); swallowing (X, XII); tongue movements (VII). C, a moment of vigilance, with outward rolling of the eye (VI); facial and ear movements (VII); listening (VIII). D, digesting (X). The only omission is the spinal accessory (XI), supplying certain neck muscles which may have been used various times in this sequence. (As summarized by Dr. Stanley Cobb, in Stiles, *The Nervous System and its Conservation*, W. B. Saunders Co.)

portion of the medulla and running to join the vagus, are probably represented in lower vertebrates by posterior rootlets of the vagus. The others, arising by a series of rootlets from the anterior cervical region of the spinal cord, are thought to correspond to spino-occipital nerves of lower forms. These fibers of spinal origin innervate the trapezius and sternocleidomastoid muscles. The fibers which join with the vagus are distributed with it to the striated muscles of the pharynx and larynx and to the autonomic nervous system.

11. Hypoglossal Nerve (XII)

The *hypoglossal nerve* is made up of somatic motor fibers which innervate the muscles of the tongue. Although it is found only in amniotes, it probably corresponds to some of the spino-occipital nerves of fishes.

The functions of the cranial nerves are cartooned in Figure 658.

XL. THE AUTONOMIC NERVOUS SYSTEM

Much of the routine work of the body, particularly of the circulatory and respiratory apparatus, of the viscera, and of the smooth muscles, is regulated by the general visceral efferent component of the nervous system, called by Langley the *autonomic nervous system*.

This visceral efferent component, in contrast with the somatic efferent, always requires two successive neurons to conduct an impulse from the central nervous system to an effector organ. Further, general visceral reflexes, for which the autonomic nervous system serves as the efferent pathway, are not under voluntary control and tend to be more diffuse and not as delicately coordinated as somatic reflexes.

1. Visceral Reflexes

The afferent neurons which communicate with the autonomic nervous system are not essentially different from those involved in somatic reflexes. Although some are visceral sensory, with their dendritic endings in internal organs, others are somatic sensory, coming from external sense organs. It is chiefly through their peripheral connections that these two types of sensory neurons may be distinguished, for both enter the central nervous system by way of the dorsal nerve-roots and both have their cell bodies in the sensory ganglia of these roots.

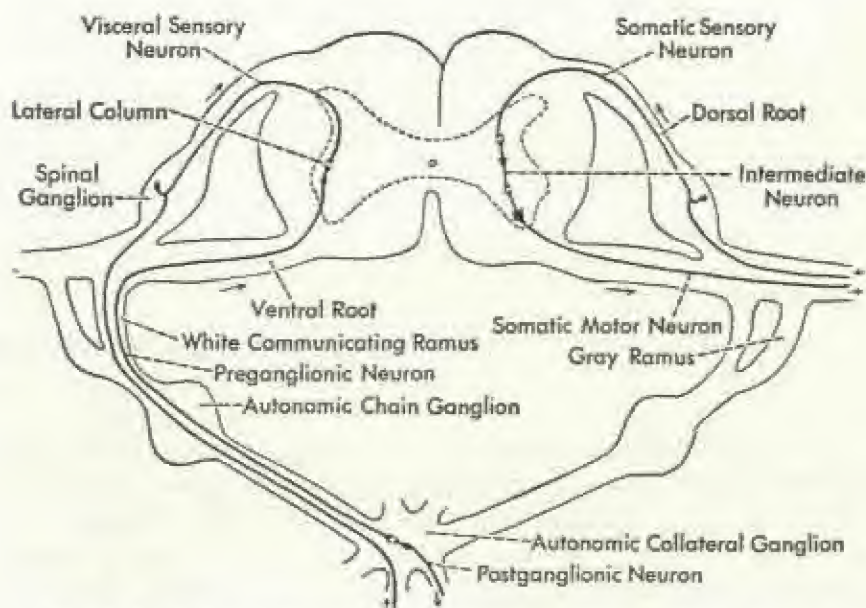


Fig. 659. Reflex pathways in the peripheral nervous system. Somatic reflex arc on the right; an autonomic reflex arc on the left. Arrows indicate courses of nerve impulses.

This similarity in the afferent components of somatic and visceral reflex arcs is not extended to their remaining elements. As previously described, in simple somatic spinal reflex arcs the sensory neuron synapses with an intermediate neuron which is entirely within the central nervous system. The intermediate neuron synapses with an efferent, or motor, neuron which has its cell body in the ventral horn of the gray matter. The neurite of the motor neuron, running out through the ventral root of the spinal nerve, extends, without interruption, to the striated muscle fibers which it innervates.

Thus the efferent pathway of a simple somatic reflex consists of but one neuron (Fig. 659).

In the case of visceral spinal reflexes involving the autonomic nervous system, the visceral motor neuron, with which the sensory cell synapses without intervention of an intermediate neuron, has its cell-body in the lateral column of the gray matter. Its neurite, which leaves the spinal cord through the ventral nerve-root, does not reach an effector but terminates instead in an outlying autonomic ganglion. Because this cell leads to a ganglion it is known as a *preganglionic neuron*. The preganglionic cell synapses with a second efferent neuron which has its cell-body within the ganglion and sends its neurite to an effector, either an involuntary muscle or a gland. This second unit in the efferent pathway is called a *postganglionic neuron*. As shown by Langley at the turn of the century, autonomic pathways probably always consist of these two successive neurons.

Preganglionic neurites are myelinated and covered with neurolemma, as are most fibers, both sensory and motor, in cranial and spinal nerves. Postganglionic neurites, on the other hand, are usually non-myelinated, having only the thin neurolemmal sheath.

2. Autonomic Outflows

In mammals the nerves which include preganglionic fibers fall into three groups, namely: cranial, thoracico-lumbar, and sacral. These are known as *autonomic outflows*, or *divisions* of the autonomic nervous system.

The *cranial division* consists of five nerves, the oculomotor, facial, glossopharyngeal, vagus, and spinal accessory, as shown in Tables XI and XII under the heading "general visceral efferent." The *thoracico-lumbar division* includes the thoracic and first few lumbar nerves. According to Sheehan the most posterior nerve belonging to this group in man is the second lumbar (L2), while in the monkey it is L3 or L4 and in both cat and dog L4. The *sacral division* is made up of the third and fourth sacral nerves in man, while it consists of sacrals one, two and three in monkey, cat, and dog.

In the cranial and sacral divisions, the autonomic ganglia, in which are located the postganglionic cell-bodies, are close to or embedded in the organs which they innervate (Fig. 660). Being near to the termination of the pathway from the central nervous system to the viscera, they are known as *terminal ganglia*.

In the thoracico-lumbar division, some of the ganglia are terminal while others are nearer to the nerve cord. Many, lying ventro-lateral to the verte-

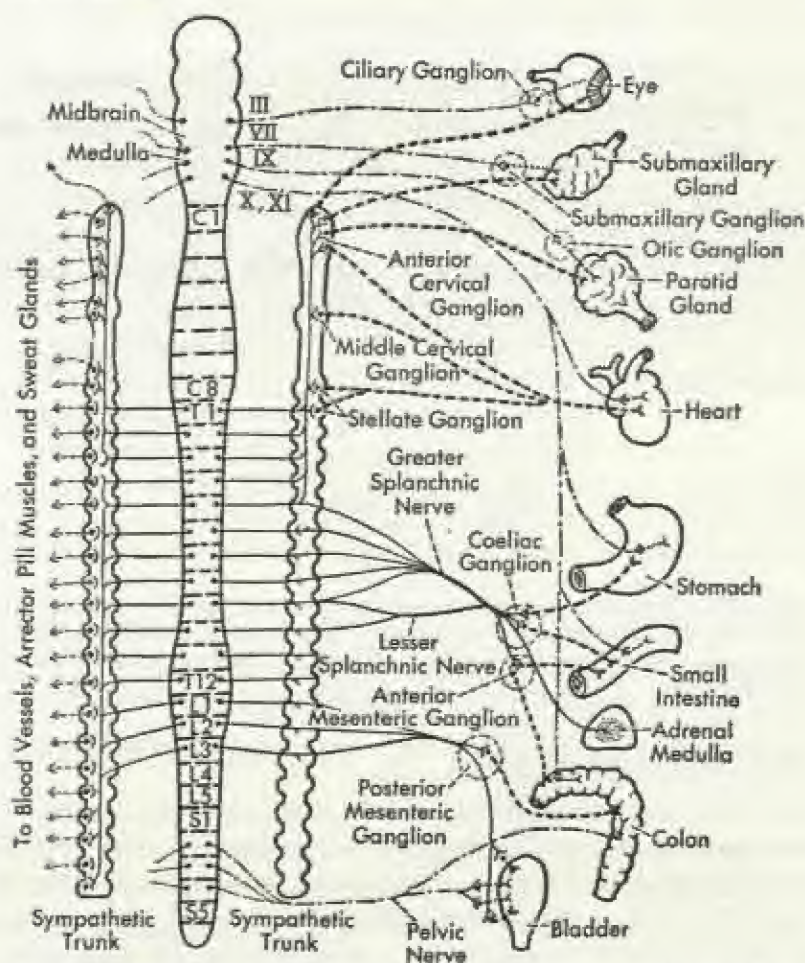


Fig. 660. Diagram of the principal autonomic nervous pathways. The parasympathetic paths are represented as follows: preganglionic neurons by dash-and-dot lines; postganglionics by dotted lines. Sympathetic paths are: preganglionic by continuous lines; postganglionics by broken lines. Pathways to blood vessels and integument shown only on left side of figure; those to other visceral structures, only on the right side. (After Bailey.)

bral column on either side, are connected longitudinally into a pair of ganglionic chains. They are known as *chain*, or *vertebral*, *ganglia*. In addition there are *collateral ganglia* lying on the dorsal aorta at the points where the three major arteries to the digestive tract arise (Fig. 661). Thus there are three types of ganglia in which postganglionic cell bodies associated with this outflow may be located.

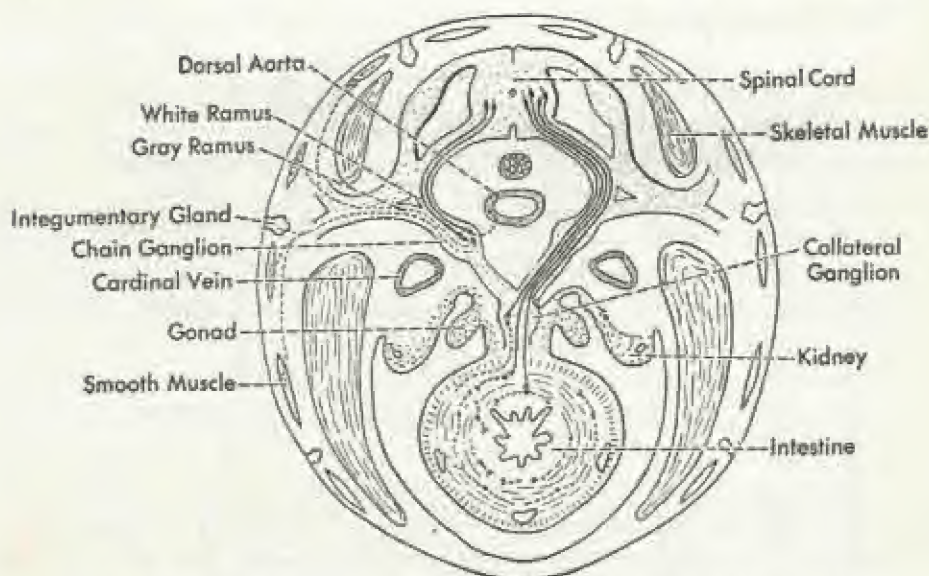


Fig. 661. Diagrammatic cross section through the trunk of a vertebrate, showing the distribution of autonomic excito-motor fibers. Preganglionics in continuous lines; postganglionics in broken lines. (After Goodrich.)

3. Thoracico-Lumbar Division

One of the characteristic features of the thoracico-lumbar outflow is the chain of vertebral ganglia, also known as the *sympathetic trunk* (Fig. 660). Each segment, beginning with the first cervical, is represented in the chain, but the eight ganglia of the cervical region have coalesced into three, known as the *anterior*, *middle*, and *posterior cervical ganglia*. Although subject to some variation, the anterior probably corresponds to the ganglia of the first four neck segments, the middle to the fifth and sixth, and the posterior to the seventh and eighth. Sometimes the first thoracic ganglion fuses with the posterior cervical to form the *stellate ganglion*.

To the sympathetic trunk preganglionic fibers are carried by the nerves which make up the thoracico-lumbar outflows (T1–L2, inclusive, in man). Each of these fibers divides into a number of branches in the trunk (Fig. 662). Usually one or more branches terminate in the ganglion belonging to the nerve through which the fiber leaves the cord, but others run anteriorly and posteriorly in the trunk and occasionally some cross to the trunk of the other side. As there is no cervical outflow, the cervical ganglia are supplied solely by fibers running forward from the thoracic region. Similarly the posterior lumbar and sacral ganglia are supplied by preganglionic fibers

which reach them by running posteriorly through the sympathetic trunk.

Between each thoracic ganglion and its spinal nerve is a *ramus communicans*, sometimes spoken of as the autonomic branch of the nerve. This ramus consists of two portions (Fig. 659). Through one part, known as the *white communicating ramus* because its fibers are myelinated, run preganglionic fibers carrying impulses from the cord to the various autonomic ganglia. Through the other portion, known as the *gray communicating ramus* because its fibers are unmyelinated, postganglionic neurites run back from the chain ganglia into the spinal nerve, through which they are distributed to sweat glands, arrector pili muscles, and the walls of blood vessels of the body wall and appendages.

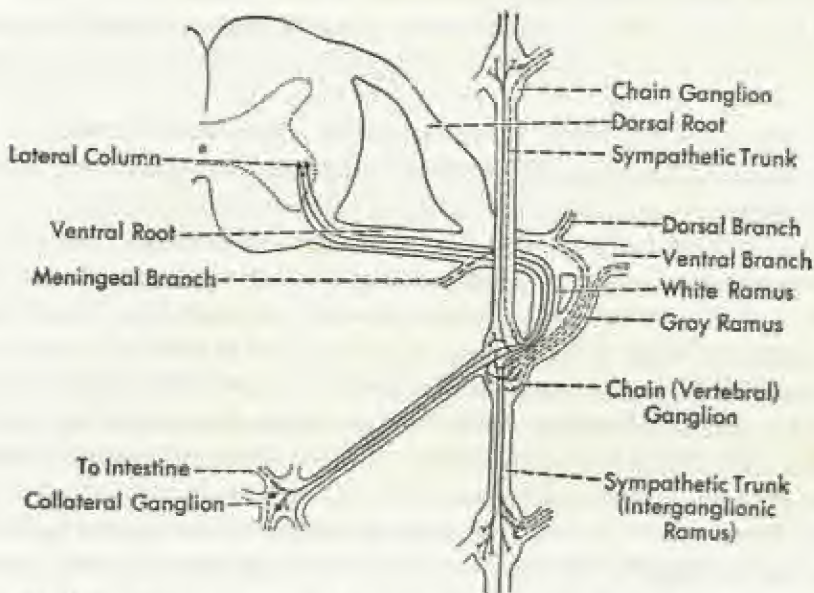


Fig. 662. Diagram showing the relations of the sympathetic ganglionic chain to the spinal cord and spinal nerves. Preganglionic fibers are shown as continuous lines; postganglionic fibers as broken lines. (After Ranson and Clark.)

As there is no cervical outflow, nerves of this region do not have white rami but they are equipped with gray rami which carry postganglionic fibers from corresponding cervical ganglia. Other postganglionic fibers from these ganglia run to the heart, the salivary glands, and the eye.

Posterior lumbar and some sacral nerves also have gray but no white rami as the thoracico-lumbar outflow ends in the mid-lumbar region.

As previously mentioned, most preganglionic fibers continue beyond the autonomic chain ganglion associated with the nerve through which they leave the spinal cord. Many run anteriorly or posteriorly to distribute to several chain ganglia. These longitudinal fibers, which connect the ganglia together into a chain, form the *rami interganglionares* (Fig. 662). Other preganglionic fibers may run across to the sympathetic trunk of the opposite side, forming groups known as *rami transversarii*.

Many preganglionic fibers, continuing through the chain ganglia without interruption, extend to collateral or to terminal ganglia. The largest collateral ganglia are the *coeliac*, *anterior mesenteric*, and *posterior mesenteric*, so called because they lie near the points where similarly named arteries originate from the dorsal aorta. The distribution of postganglionic fibers from these various ganglia is shown in Figure 660.

The visceral nerves, supplying the internal organs, include not only preganglionic and postganglionic fibers of the autonomic nervous system but also visceral sensory fibers which run from these organs to the spinal cord. These sensory fibers, which reach the spinal nerves by way of the white rami, extend from the internal organs to the spinal cord without interruption.

The fibers of the autonomic nervous system are prone to form plexuses by anastomosing together. Chief among these plexuses are the *cardiac*, *coeliac*, and *hypogastric*, the names of which indicate their associations. The largest of these is the coeliac, or *solar*, plexus in which lie the coeliac and anterior mesenteric ganglia. This plexus includes fibers associated with both the thoracico-lumbar outflow and the vagus nerve as well as visceral sensory fibers. From this plexus, fibers radiate to the stomach, small intestine, liver, pancreas, colon, spleen, kidneys, adrenal glands, gonads, and associated blood vessels. A "blow on the solar plexus," it is obvious, is likely to have far-reaching repercussions quite as effective as the traditional "monkey wrench thrown into the machinery."

4. Double Autonomic Supply

Most of the viscera have a double autonomic nerve supply, each organ being innervated by either the cranial or the sacral outflow in addition to the thoracico-lumbar (Fig. 660). Impulses transmitted to an organ by the thoracico-lumbar division produce effects that differ from those brought about through the activity of the cranial or sacral outflows. Further the cranial and sacral outflows resemble one another, but differ from the thoracico-lumbar, in their responses to certain drugs, for example, adrenalin, atropin, and pilocarpin. It is convenient, therefore, to group the cranial

and sacral outflows together as the *parasympathetic system*, in contrast with the thoracico-lumbar division, or *sympathetic system*. Examples of this double innervation are the autonomic supplies to the eye, heart, and small intestine.

The parasympathetic innervation of the *eye*, through the oculomotor nerve, brings about reduction in the size of the pupil and accommodation for near vision. The sympathetic supply, by way of the anterior cervical ganglion, causes dilation of the pupil.

The *heart* is slowed down (inhibited) by impulses brought to it through the vagus nerve (parasympathetic) but its beat is accelerated and increased in force by sympathetic impulses, which for the most part pass through the stellate ganglion.

Intestinal peristalsis, on the other hand, is increased by the vagus and inhibited by its sympathetic nerves, which come mainly from the coeliac and anterior mesenteric collateral ganglia.

5. Comparative Anatomy of the Autonomic System

In amphioxus there is no involuntary nervous system, but in cyclostomes ganglia unconnected by means of interganglionic fibers are established in the body region. Elasmobranchs and perennibranchiate amphibians show an advance, in that a network of fibers connects some of the trunk ganglia with each other. In teleosts a thin trunk-line of interganglionic fibers is present with frequent transverse rami, while the Vth, VIIth, IXth, and Xth cranial nerves form a bulbar outflow that extends the involuntary system into the head. In anurans only the Xth nerve is involved in the parasympathetic part of the involuntary system. It is not until the amniotes are reached that the primary involuntary system of the trunk becomes definitely extended to both cranial and sacral regions.

In addition to this nervous regulation of visceral activities, there is considerable non-nervous control through hormones produced by endocrine glands, as when secretin from the intestinal wall stimulates the flow of the pancreatic juice from the pancreas.

Again the close connection between the autonomic system and hormonal control is shown by the fact that at the time when the neuroblasts, or embryonic neurons, migrate out from the thoracico-lumbar region to form the involuntary ganglia, they are accompanied by certain so-called *chromaffine cells* that have the power to secrete adrenalin. These cells eventually become localized in the suprarenal glands, where they produce adrenalin, a hormone which stimulates fibers of the sympathetic portion of the autonomic nervous system.

The will, or the exercise of the voluntary apparatus, can affect the action of the autonomic system under certain circumstances, as for example, when man, as contrasted with animals, sets up definite arbitrary times for eating and sleeping. This is conscious control of a more or less unconscious performance. Inhibition of the unconscious machinery of digestion can be brought about indirectly by conscious worry originating in the realm of the voluntary nervous apparatus.

Ports of Entry—Sense Organs

I. IN GENERAL

Communication with the outside world is made possible by *sense organs* that form the most peripheral part of the nervous system.

They are essentially *environmental organs* that by way of the sensory nerve fibers with which they are connected receive and transmit impressions of what is happening in the surroundings. By themselves they do not sense or feel these happenings, for they are simply avenues of approach to the central nervous system which is the particular part of the body endowed with the power of sensation. When one, for example, "feels" a pin-prick in the finger tip at the point where the contact is made rather than in the brain where the sensation actually occurs, it is because he has become accustomed to refer all sensations to the point where the stimulus originates, and mistakes the gun for the man behind the gun. One does not see *with* a pair of glasses but *through* them.

It all goes back to remote evolutionary days when the function of sensation actually was located at the surface in that part of the body exposed directly to outside bombardment. Although the receptive sensory tissues of a living animal are originally ectodermal in origin and external in position, they do not remain in this exposed situation but in the course of time become for the most part buried within the protective body, in this way being shielded from direct impact with the strenuous and constantly changing outside world.

The withdrawal of the central nervous system from direct external influences necessitates the establishment of peripheral nerves in order to retain connection between the central nervous apparatus and the surrounding environment. Since nerve fibers in themselves are not so well adapted for the reception of outside messages as for the transmission of them, specialized sensory structures that are outposts, like sentries on guard around a camp, are required to keep in touch with the environment.

These intermediary structures between the organism and its surroundings are commonly known as "sense organs," although it is preferable to call them *receptors*, since not all impressions received through them result in sensation. In fact sensation is only an incidental result of receptor excitation.

1. Stimuli

A *stimulus*, which is something that a receptor receives, is defined by Stiles as "a change, physical or chemical, which is capable of producing physiologic reactions."

It may come from the outside in the form of environmental changes of various sorts, or it may arise from processes going on within the organism, as when the production of carbon dioxide in the blood stimulates the respiratory center in the medulla with the result that the muscles involved in breathing are set into action.

The essential thing about any stimulus is the element of *change*, or the fact that something different in kind or degree is taking place in the surroundings of an animal.

Constantly repeated or long enduring stimuli fail to register sensation, as for example when the hum or roar of city traffic fades with fatiguing repetition and becomes noticeable again only when there is a change in the character or intensity of the sounds produced. It is possible, therefore, to become oblivious to extraneous happenings that are irrelevant to certain sense organs involved, thereby gaining a high degree of efficiency in the reception of specific stimuli upon which the attention is focussed.

As pointed out long ago by Helmholtz, sense organs cannot give a true picture of the actual environment in which we live, but only of *the changes taking place in it*.

The continuous regularly repeated heart-beat, or the constant waving of cilia do not require a fresh stimulus for every muscular movement that they make. Neither do processes of growth and repair call for sensory stimulation.

2. Receptors

Receptors are generally cells or organs that are specialized to take in impressions of a *single kind*, and no others (Müller's Law). Such receptors are said to be "adequate" for the stimulus in question. The eye is adequate for light, and taste organs for the chemical stimulation of dissolved substances, but neither is adequate for the reception of sound waves. This exclusive adaptation to only one type of stimulation is a very great advantage

since in this way protection is gained against unnecessary annoyance arising from stimuli other than the one to which the receptor in question has become adapted. The sensory elements of eyes and ears, for example, while retaining a clear pathway for exposure to the stimuli of light and sound respectively, are meanwhile protected from chemical and tactile stimulation, as well as from temperature changes. In the same way smell and taste organs, although in an ideal situation to be affected by gases and liquids, are not particularly exposed to mechanical contacts or to the impact of waves of sound or light.

Many receptors that are entirely adequate for their own kind of stimuli can gain relief from excessive or incessant bombardment of stimuli by being temporarily excluded from even their own particular sort of stimulation. Thus it is possible to shut out light for the time being by closing the eyes, and to cease from tasting things by keeping the mouth shut.

Sometimes a receptor is acted upon by a stimulus for which it is not adequate or appropriate. When menthol is rubbed into the skin a feeling of cold results instead of the usual chemical response of smell, or if a vibrating tuning-fork is placed on the tip of the tongue, instead of hearing a sound, the result is a tickling sensation which is a form of touch-response. In these instances the thermal sense endings in the skin are *inadequate receptors* for the chemical stimulation produced by menthol, and the tactile buds on the tip of the tongue are inadequate receptors for the sound waves from the tuning-fork. In both cases it is the central nervous system and not the stimulus or the receptor that is responsible for the particular sensation that is experienced. It is entirely possible for sensation to occur in the complete absence of a receptor, as in dreams, or when the stimulus comes in through a port of entry not adequate for it.

In any case the impulses that give rise to sensations do not originate with the receptors but are simply transferred through them to the sensory headquarters within. When we blame our innocent feet for being weary after tramping for hours through a museum or art gallery, the inaccessible brain within calls no attention to its guilty self but lets the illusion pass without protest.

When one realizes how easy it is to have sensory illusions of all sorts, and how variable the central judgment may be upon the "evidence of the senses," not only in the case of different individuals reacting to the same circumstances but also of the same individual at different times, it is small wonder that lawyers have difficulty in extracting the truth even from perfectly honest sworn witnesses, since natural limitations compel us all to "see through a glass darkly."

3. Response

Protozoans have no hook-up between sense organs and a central nervous system, but nevertheless are in responsive communication with their environment, and may, therefore, be properly referred to as *sensoria*. The same is true of plants, which have no nerves, although responding definitely to environmental stimuli, such as light, temperature, moisture, and gravity. In fact *irritability*, or the capacity to respond to stimuli, is an essential universal property of protoplasm. The sensory receptors of higher animals are simply cellular structures that have specialized in this general endowment of irritability.

Response to stimuli resulting from environmental changes may take the form of (1) muscular contraction; (2) glandular secretion, or (3) even the more involved processes of psychic performance.

There are upper and lower limits in the receptive range of human sense organs. Thus, the range of vibrations which stimulate the human ear as sound lie approximately between 16 and 40,000 per second, while the range of the visible spectrum to the human eye is between 481 billion ether waves per second at the red end, and 764 billion at the violet end. Outside of these extremes human receptors are ineffective with respect to either sound vibrations or light waves, and except within such limits one can neither hear nor see.

4. Sensory Range in Animals

The sensory range of animals other than man is usually not only unlike that of man but may also extend beyond it. Cats, for example, are known to respond to higher tones than are perceptible to human ears; ants, subjected to a field in which light is broken up by a prism into components of the spectrum, arrange their exposed pupae with reference to ultra-violet light that is invisible to the human eye; dogs perceive a repertory of odors of which man knows nothing; and house flies distinguish the difference between cane sugar and saccharin which to the human tongue may taste alike.

Birds upon a battlefield, it is reported, are apparently not alarmed by the terrible crash of exploding cannon, continuing to sing and to fly about as usual since the whole unusual performance is quite beyond their customary range of reception. The picture of a mouse, however lifelike, awakens no interest when placed before the eyes of a hungry cat.

The character of any sensation depends not on the nature of the impression received but on the properties of the brain cells to which the impression is referred.

Owing to the specialized receptivity of different kinds of receptors for particular stimuli, and the largely variable subjective element that has so much to do with the use made of sense organs, it is extremely uncertain how far our knowledge about the sensory life of animals other than ourselves is dependable. Even in the case of other human beings with a sensory equipment apparently quite like our own, we can only infer what the sensations experienced by mutual stimuli are like.

It becomes necessary with regard to animals having receptors and a central apparatus unlike that of man to resort to observation of objective behavior resulting from the application of some particular stimulus, in order to make any reasonable guess as to how they "feel" in such experimental circumstances. Behavior, moreover, is by no means always a safe criterion on which to depend, for a responding animal may not do what man or some other animal might do under the same conditions. Similar movements do not necessarily express similar sensations. For example, when a friendly dog wags its tail, it portrays an entirely different state of mind from that of an excited tiger, lashing its tail back and forth. It is especially embarrassing for man, whose tail is only an evolutionary memory, to try to pass active objective judgment on the feelings that find expression in tail movement.

Naturally the more unlike man an animal is, the more uncertain must be the human interpretation of the world in which the animal lives. The classical story of Apuleius of *The Golden Ass*, in which the hero by witchcraft experiences an interlude of being an animal, suggests to the exploring biologist an illuminating line of imaginary research and speculation.

5. Accessory Structures

In general the sensory endings of afferent nerve fibers are either free or encapsulated. *Free nerve endings* terminate among the epithelial cells, connective tissue elements or muscle fibers without any specialized cells surrounding them. *Encapsulated endings* are enclosed by groups of cells of varying complexity. Rallying to the aid of the specialized sensory cells, which are the essential receptors, is an army of various accessory cells serving as nourishers, protectors, and magnifiers in the make-up of the complicated sense organs.

Ectodermal receptors may be scattered in integumentary sense organs, or be clustered together and surrounded by cells and tissues, largely of mesodermal origin, that are responsible for the elaborate differences which characterize the various sense organs.

As might be expected, the least morphological complication is found in receptors of the more primitive aquatic animals. The transition to land life,

with consequent access to a wider range of stimuli, has been invariably accompanied by an increased differentiation in the structure of the receptor organs; nevertheless among the highest land vertebrates the essential sensory receptor cells of elaborately specialized sense organs, such as the ear, are still bathed in fluid as are the more primitive receptors of aquatic forms.

In nearly all cases the sensory receptors are particularly protected from mechanical injury. Eyes are housed in sunken skeletal orbits; the sensory parts of the ears are entirely embedded within cartilage or bone of the cranial wall; the olfactory epithelium is safely concealed upon the inner wall of cavernous nasal pits; the organs of taste are inside the mouth cavity behind closing jaws; even the cutaneous organs of temperature, pain, touch, and pressure, which are located in the exposed skin, are in many instances either sunk below the surface, or surrounded by an individual barricade of non-sensitive, protective cellular materials.

II. CLASSIFICATION OF RECEPTORS

The old subjective classification of the sense organs into touch, smell, taste, sight, and hearing is no longer sufficiently inclusive, for there are nearer twenty-five than five different kinds of receptors that can be distinguished in man alone, not to mention additional ones which characterize animals other than man.

By considering receptors in relation to their adequacy for particular stimuli rather than the sensations produced through them, an objective rather than a subjective basis is found for their classification, making possible not only more accurate description but also the inclusion of certain known receptors for which no corresponding sensation is recognized.

Classifying receptors first in accordance with the source of the stimuli for which they are adequate, there are three major groups, designated by Sherrington as *exteroceptors*, whose stimuli come from the outside; and *proprioceptors*, and *interoceptors*, whose stimuli arise within the organism itself.

Exteroceptors receive mechanical, chemical, and radiant stimuli. The more deeply seated proprioceptors have to do with the control of the musculature and the working of parts of the body upon each other, while interoceptors are associated primarily with the digestive tract and things like food within but not a part of the body.

Exteroceptors are environmental organs proper, dealing with the objective outside world, while proprioceptors and interoceptors are more subjective and personal, leading to sensations more difficult to define, such as

hunger, thirst, fatigue, muscle tonus, sexual excitation, visceral pain, nausea, and the general sense of well-being.

Although it is possible for the physicist by means of such gadgets as dynamos, thermopiles, telephones, chemical solutions, photoelectric cells and the like, to convert all the various stimuli arising in the external environment to the common denominator of electric energy, man and animals are not provided with any specific receptors for the electric current itself. If they were, universal electric sense organs might replace the diversity of receptors which have been evolved.

Table XIII gives an arrangement of receptors with the stimuli for which they are adequate and, so far as possible, the sensations which in each case result.

TABLE XIII. Classification of Receptors

I. Outside sources <i>Exteroceptors</i>		
1. Mechanical stimuli		
a. Temporary contact	Tangoreceptors	Touch, Pressure
b. Vibratory contact	Phonoreceptors	Hearing
c. Intensive contact	Algesireceptors	Pain
d. Currents of water	Rheoreceptors	Orientation
2. Chemical stimuli		
a. Gases	Olfactoreceptors	Smell
b. Liquids	Gustoreceptors	Taste
c. Irritating substances	Irritoreceptors	Irritation
3. Radiant stimuli		
a. Thermal	Caloreceptors	Heat
b. Thermal	Frigidoreceptors	Cold
c. Photic	Photoreceptors	Sight
II. Inside sources		
1. Muscular control	<i>Proprioceptors</i>	Tonus
2. Alimentary control	<i>Interoceptors</i>	Hunger, Thirst

For convenience in description receptors may be grouped into :

1. Cutaneous sense organs
2. Special chemical sense organs
3. Gravity organs
4. The master senses of hearing and sight
5. Internal sensory mechanisms

III. CUTANEOUS SENSE ORGANS

The sense organs of the vertebrate skin include a variety of kinds, among which are organs of touch and pressure, temperature, pain, and in some aquatic forms, taste, and lateral-line organs that are stimulated by currents of water.

Some of these cutaneous organs also invade the mucous membranes that line the passage-ways into the body, particularly in the transitional region between the exposed skin on the outside and the moist mucous lining within.

There is an evolutionary tendency for cutaneous receptors to withdraw from their original position directly at the surface of the skin. This is particularly true in land forms whose skin is exposed to dry air, thus necessitating ecdysis or the periodic removal of the dead outer corneal layer. It is an obvious advantage when ecdysis does not disturb sense organs located in the skin, since specialized neurons are not adapted, as are less elaborated cells, for renewal by mitosis. In most aquatic vertebrates where there is not much need for ecdysis the primary superficial location of the sense receptors is common. Upon assuming a deeper position sensory neurons extend their receptive dendritic processes towards the surface and the source of stimulation. These processes may either end freely between the cells of the skin, or they may terminate in intimate relation with some sort of an accessory apparatus that acts as a *stimulator*, or non-nervous mechanical intermediary between the receptor itself and the stimulus. The stiff "whiskers," or *vibrissae*, of a cat, for example, transfer the stimulus of mechanical contact to deep receptor neurons, dendrites of which form a brush or net around the embedded ends of the vibrissae. Cutaneous receptors are the most numerous and widely scattered of any sense organs.

1. Tangoreceptors

The tactile sense is the most universal and unavoidable of all the means of communication between the organism and its environment. While it is quite possible to close the eyes and ears against sights and sounds, or to avoid the chemical stimuli that lead to taste and smell, it is not so easy for a body of three dimensions to escape from contact with the gases, liquids, and solids surrounding it.

Tangoreceptors give an idea of the weight, size, shape, surface texture, and general character of objects within reach. *Touch* is not only the most universal of the senses, but it is the great *confirmatory sense*, bearing supplementary witness particularly to the major sense of sight. A baby, for example, never discovers its toes by simply gazing at them, for it is only when it

accidentally grasps them in its exploring fingers that it joyfully recognizes them as its own.

When touch is sustained beyond transient contact, it becomes interpreted as *pressure*. Although in many instances the same receptors give the sensations of both touch and pressure, the sense of touch is more definitely localized both in time and space and varies in intensity from that of pressure.

While widely scattered, tangoreceptors are by no means equally distributed throughout the skin, but are placed more abundantly in locations where they are most likely to come into contact with external objects. Thus in man the knee is more sensitive to touch or pressure than the thigh, and the friction areas on the inside of the hands and feet than on the scalp. The concave surface of the curving tail of the spider monkey, *Ateles* (Fig. 205), is bare of hairs and richly supplied with organs of touch, because this active animal makes constant tactile use of the tail in its arboreal adventures. The belly of climbing animals like squirrels is particularly well supplied with tangoreceptors, and even on the inside of the forearm of the human fetus (Fig. 198) there are transient tactile hairs which hark back to the dim past when arboreal ancestors clung to branches of trees.

Scaly reptiles, in addition to the development of a highly tactile tongue, have either non-sensitive corneal "hairs" similar to those on a bee, that act mechanically as stimulators upon the sensory receptors embedded in the skin below, and are shed at ecdysis with the scales on which they grow, or else certain of the scales are penetrated by small pores, through which cutaneous tangoreceptors gain access to outside contacts.

Not much is known about the organs of touch in the skin of fishes and amphibians. Certain sensory terminal buds have been demonstrated in the connective tissue at the base of the fins in elasmobranchs, while there is little doubt that the barbules dangling around the mouth of such bottom-feeding fishes as the catfish, *Amiurus*, have a cellular equipment which enables them to act as "feelers." In general the scaly skin of fishes and reptiles excludes tangoreceptors.

In amphibians the mucous membrane covering the tongue is sensitive to touch, and in snakes there are sense cells in the flickering protrusible forked tongue, although specialized tangoreceptors in the skin have not been demonstrated in these animals. It is in mammals that tangoreceptors reach their greatest elaboration and have been most studied.

Free nerve endings may extend between the cells of the epidermis as far as the stratum granulosum. They are especially abundant in the outer root sheaths of hair follicles which are possibly the only tactile organs for much of the integument (Fig. 663).

Of the types of tangoreceptors that make use of accessory non-nervous structures the simplest are *Merkel's corpuscles* (Fig. 664) in which the exposed ends of the dendrites form cups, each fitting under an epithelial *stimulator cell*. Whenever such cells are agitated by contact, the stimulus is received by the cuplike enfolding tips of the nerve fibers and transferred to

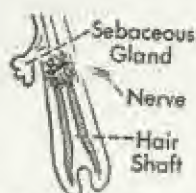


Fig. 663. Nerve endings in a hair follicle.

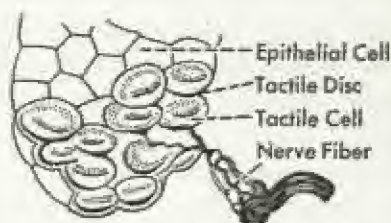


Fig. 664. Merkel's tactile corpuscle, from the snout of a pig. (After Tretjakoff.)

the brain, with the resultant sensation of touch or pressure. In this case the non-nervous stimulator cells are larger and more likely to effect a contact with something outside than free intercellular nerve endings would be. Merkel's corpuscles are particularly abundant on the exploring tip of a mole's nose or the rooting snout of a pig.

In hairless portions of the skin there are encapsulated tactile endings, located chiefly in the outermost region of the derma. Included among these are: the end bulbs of Krause, the Vater-Pacinian corpuscles, and Meissner's corpuscles. Krause end bulbs are found in the sensitive mucous membranes of the mammalian tongue and lips, in mammary glands, in the conjunctiva of the eye, in the corium of the finger tips, in the external genitalia of man, and in the moist snouts of grazing cattle (Fig. 665). They may be cold-receptors instead of tactile organs.

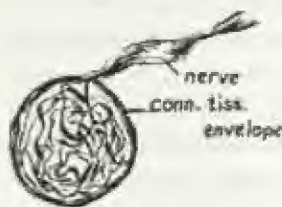


Fig. 665. A Krause end-bulb, from the edge of the conjunctiva in man. (After Wiedersheim.)

Vater-Pacinian corpuscles occur in the subcutaneous layers of the skin, as well as even deeper in tendons and joints, in the pleural walls, around the larger blood vessels in the diaphragm, and in the peritoneum and mesentery of the body cavity (Fig. 666). The Vater-Pacinian corpuscles are the largest and microscopically the most elaborate of all tangoreceptors. The terminal branches of the receptor neuron are enwrapped by successive layers of connective tissue, like a Dutch vrouw's petticoats, the whole structure being easily visible to the naked eye.

A similar but less elaborate mechanism, *Grandry's corpuscles* (Fig. 667), found only along the margins of the beaks of birds like sandpipers and ducks, consists of two large, disclike, non-nervous stimulator cells with nerve endings from a sensory neuron sandwiched in between them, the whole packet being surrounded by an envelope of connective tissue.

The so-called *Herbst corpuscles* (Fig. 668), likewise found only in the mouth-parts of birds, consist of two rows of non-nervous stimulator cells arranged on either side of a neural core within a capsular sheath. They are distributed not only within the mouth cavity but also between certain muscles and in areas of the skin that are comparatively free from feathers.

Finally, *Meissner's corpuscles* (Fig. 669), which occur in the friction areas of the skin of primates, resemble highly elaborated Grandry corpuscles, but instead of two, there is an irregular pyramid of non-nervous stimulator cells, interlaced by the branching ends of sensory receptor neurons, the entire mass being enclosed in a sheath. When pressure is applied to a Meissner cor-

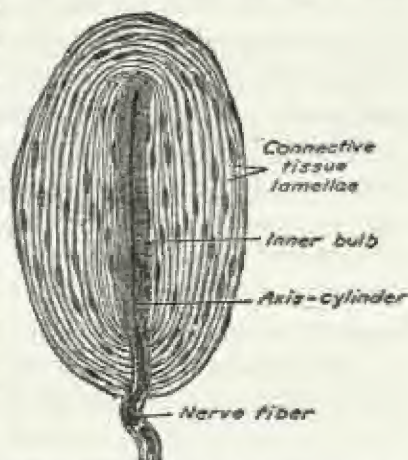


Fig. 666. A Pacinian corpuscle. (From Smith and Copenhaver, *Bailey's Text-Book of Histology*, copyright 1944, by permission of Williams and Wilkins, publishers.)



Fig. 667. Grandry's corpuscle, consisting of two sensibulator cells with nerve endings between them. (After Dogiel.)

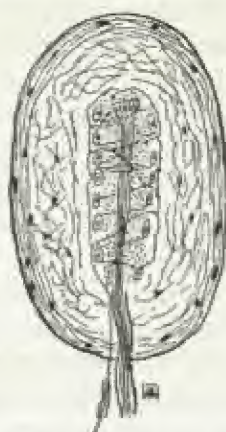


Fig. 668. Herbst's corpuscle from tongue of a duck. (After Plate.)



Fig. 669. Meissner's tactile corpuscle within a papilla of the skin of the hand. (After Ranvier.)

puscle the whole apparatus compresses like an accordion and the squeezed arborizations of the tangoreceptor send along to the brain the sensation which is translated as touch or pressure. Meissner corpuscles are also the sense buds that form the *sensory papillae* just below the epidermis along the friction ridges of the finger tips (Fig. 139), which make the fingers such delicate and effective organs of touch. Removing a glove before shaking hands has a physiological as well as a social reason back of it.

While tangoreceptors are usually concerned only with actual contact, there is some evidence that they aid in determining the presence of nearby objects, possibly through pressure resulting from intervening air currents. A blind person, for example, whose tactile senses have become compensatingly sharpened, is uncannily aware of the neighborhood of a wall which he may be approaching before he bumps into direct contact with it.

The fact that the delicate skin of infants is evidently more sensitive than that of adults is partly due to the stretching of the growing skin, resulting in an increase of the spaces between the tangoreceptors.

Discrimination in touch varies in different regions of the skin. It may be measured by recording the minimal distance at which the fine points of a lightly placed pair of calipers give the impression of two points of stimulation instead of one. See Table XIV.

TABLE XIV. Discrimination in Touch
(From Barton-Opitz)

	<i>mm.</i>
Palm of the last phalanx of finger.....	2.2
Palm of the second phalanx of finger.....	4.4
Tip of nose	6.6
Back of second phalanx.....	11.1
Back of hand	29.8
Forearm	39.6
Sternum	44.0
Middle of back	67.0

2. Thermoreceptors

Every animal and plant has an optimal range of temperature in which it can most successfully carry on its activities and upon which its distribution over the face of the earth very largely depends. Whenever the temperature of the environment departs from this optimum the organism becomes increasingly handicapped, until finally extremes may be reached that make life no longer possible. The range of temperature in which organisms can

remain active is somewhat less than that in which they can remain alive. Thus, hibernating animals recover from the torpor produced by extreme cold, as well as from the rigor of inactivity resulting from extreme heat, if cold and heat are not too prolonged or excessive.

The cause of death is not the same at the two extremes of excessive temperature. An *Amoeba* when subjected to gradually increasing temperatures at first becomes more active, but later entirely withdraws its extended pseudopods until it exposes the least possible surface, finally dying from the coagulation of its protoplasm. If the temperature is slowly lowered from the optimum, the pseudopods remain extended and movement becomes more and more sluggish until in the end the animal freezes in an expanded condition.

Organisms that contain very little water, like seeds and highly desiccated animals, can withstand very low temperatures, even freezing, without losing the ability to resume activity eventually. On the other hand some algae and insect larvae, probably as the result of long periods of continuous adaptation and selection, are able to exist under extremes of high temperature such as occur in hot springs, which are ordinarily fatal to most forms of life. For many years Brues has carried on special observations on the curious and unusual inhabitants of hot springs. He reports some astonishing instances of the Dantesque organisms that thrive in these aqueous infernos.

Davenport says of the distinction between endurance of extreme cold and extreme heat, "the effect of high temperatures is principally *chemical*, involving the living plasma; that of low temperatures is principally *mechanical*, involving the water of the body."

Changes in environmental temperature act as stimuli to organisms, by means of which their behavior is largely regulated. Frogs, which ordinarily swim at the surface of the water, take to the bottom when the temperature drops to about 50° Fahr. Dolbear discovered that tree crickets, *Oecanthus*, at 60° Fahr. chirp 90 times per minute, varying four chirps to every degree of deviation from that standard. At 55° the number of chirps is 71, and at 75°, 150 chirps per minute, showing that these vociferous insects are so absolutely dependent upon the exact degree of temperature in which they find themselves, that they constitute an audible thermometer of considerable accuracy.

A similar responsiveness to shades of temperature is exhibited by those amphibian Romeos, frogs, toads, and hylas, when they are staging their amorous serenades in the spring of the year.

Thermoreceptors are almost all restricted to the skin. Variations of heat and cold are not felt in the digestive tube except in the transitional mucous

membrane at either end. Thermoreceptors are in most cases free nerve endings that are confined to the skin, being absent in the viscera. When a gulp of hot coffee "feels hot all the way down," it is because thermoreceptors in the skin are stimulated from the inside so that the sensation is erroneously referred to the esophagus.

There are two types of thermoreceptors, namely, *caloreceptors* and *frigidoreceptors*, which transmit stimuli resulting in the sensations of warmth and cold respectively. The former lie deeper in the skin and are less numerous than the latter. Degrees of temperature are registered by a thermometer as a continuous series, but there is a point of demarcation between thermoreceptors at which caloreceptors hand over the reception of stimuli giving rise to temperature sensation to frigidoreceptors.

The caloreceptors upon the cheeks and forehead are highly receptive, as are those on the palms of the hands, which are naturally spread out towards an open fire on a cold day. They, as well as frigidoreceptors, are practically absent from the front face of the eyeballs, although receptors for pain, *algosireceptors*, are abundant there. In fact caloreceptors are frequently confused with algosireceptors, although frigidoreceptors and tangoreceptors are apt to be more closely associated together.

Owing to the proximity of dermal sense organs to each other, and the irregular way in which they are intermingled over the surface of the skin, accurate discrimination between the sensations produced by their stimulation is very difficult.

In the case of thermoreceptors the response resulting from stimulation is particularly conditioned by the *number* of receptors involved. The total effect experienced, for example, when an exploratory foot is plunged into a cold bath is quite different than when the whole body is submerged at once.

Confusion may also arise with respect to the stimuli that excite the temperature receptors, since the previous condition within the body immediately before change in temperature occurs plays a hangover part in determining the resultant feeling. For example, if one hand is immersed for a few moments in ice water at the same time that the other is thrust into hot water, and then both are withdrawn and plunged together into tepid water which is intermediate between the extremes, the former hand will "feel" warm and the latter cold, although both are being subjected to the same thermal stimulus.

Goldschneider, one of the first to study thermoreceptors thoroughly, located with meticulous exactness in repeated trials on his own skin warm and cold "spots" over definite small areas (Fig. 670), and then, with commendable scientific zeal, cut out pieces of this carefully charted skin which,

after sectioning and staining, he subjected to detailed microscopic examination. He found separate distinct nerve terminals that corresponded to the warm and cold spots, and drew the conclusion that the real thermoreceptors were distinct from each other.

Little is known of thermoreceptors aside from free nerve endings, particularly in vertebrates other than man. Almost nothing is known of these organs in non-vertebrates. In the cornea and conjunctiva of the eye, which are sensitive to cold but not to heat, numerous end bulbs of Krause are found. These are suspected of being frigidoreceptors. Ruffini endings, each the interlaced minute terminal branches of a single nerve fiber, are abundant in the eyelids, which are particularly receptive of heat, and probably are rightly to be classified as calorereceptors.

That thermoreceptors are distinct from other cutaneous sense organs is well established, since they not only have a differential distribution, but also behave differently upon being subjected to anaesthesia. Cocaine applied to the skin temporarily destroys the effectiveness of tangoreceptors and algesireceptors, but leaves thermoreceptors unaffected. Following transplantation operations too, the invasion of the newly-formed skin by different receptors is not simultaneous, the sense of touch being the first to be reestablished, followed by the sense of pain, and finally by the temperature senses.

Temperature discrimination in different parts of the body has been tested with the conclusion that calorereceptors of the eyelids are able to register a difference of $\frac{1}{20}$ of a degree centigrade, the red lips, $\frac{1}{10}$, the outside of the arm, $\frac{1}{4}$, and the palm of the hand, $\frac{1}{2}$ of a degree centigrade.

3. Algesireceptors

Pain is felt through definite specialized free nerve endings termed *algesireceptors*. Painful sensations are also experienced whenever excessive stimulation is applied to sense organs other than algesireceptors. "The constantly smouldering embers of sensibility," says Foster, "may at any moment be fanned into the flame of pain." Thus one speaks of a "piercing tone" as



Fig. 670. Outlines of heat spots and cold spots. Heat spots are indicated by dark diagonal shading; cold spots by light dotted shading. There is a slight overlapping in a few places. (After Goldschneider.)

painful, as well as a too brilliant light, immersion in ice water or scalding water, or too strongly applied pressure. In all these cases the painful sensation is received through stimulatory channels already established for other uses than that of giving warning of unpleasantness by pain.

Messages of pain usually demand corrective attention, since they indicate that something has gone wrong. In this sense Sherrington's term of *nociceptors*, or receptors concerned with injuries, is particularly applicable. It is far more important, much as we dislike pain, to be warned of injury in time than to be regaled uninterruptedly with delights optical, auditory, tactile, or chemical, as the case may be, that constantly assail other sense organs, and which rarely if ever admit stimuli that are fatal to life. Algesireceptors, therefore, play a peculiarly important rôle in safeguarding the well-being of the individual. They are in consequence very numerous and widespread, not only over the skin but also in underlying organs.

It has been estimated from careful mapping of certain cutaneous regions that in the entire skin of a normal human adult there are present 30,000 calorereceptors; 250,000 frigidoreceptors; 500,000 tangoreceptors; and 4,000,000 algesireceptors. This is a ratio of approximately 2:13:25:200, indicating how far algesireceptors outnumber all the others.

When it is remembered that excessive stimulation of any sensory receptor may register warning pain, it will be seen that the provision for pain sensations is beneficently generous. So elaborate an equipment for the detection of pain is far more effective in man than in other animals because the central nervous system where painful stimuli are registered is much more highly developed than in other vertebrates. The fact that fishes probably feel the hook very little allows Isaac Walton to rest in peace and not turn over in his grave.

Sometimes a part of the body, while retaining a high degree of touch or pressure receptivity, is comparatively non-sensitive to pain, as for example the inner wall of the cheek. It is not easy to localize pain at the exact point of stimulation. A toothache may seem to involve the entire jaw, or a cinder the whole eyeball, while lame chest muscles frequently are interpreted as sore lungs.

Fortunately many injuries like wounds do not result in pain in proportion to their extent. For instance the chief pain from the amputation of a leg or arm has its origin in the stimulation caused by cutting the algesireceptors located in the skin. The cortical cells of the brain itself are insensitive to mechanical contact. There are no specific stimuli for pain or localized centers in the brain for painful response alone, as are known to exist for the senses of sight, hearing, smell and taste.

4. Rheoreceptors

Certain cutaneous sense organs, arranged around the head and down the sides of the bodies of fishes and aquatic amphibians, are termed *rheoreceptors*, or water-current receptors, which aid the animal in orientation to flowing water.

In embryonic development and adult structure these organs appear to be related to the organs of hearing. Further they probably detect vibrations in the water. Consequently they are often classified with the ears as parts of the *acoustico-lateral system*.

Primitively a rheoreceptor organ, known as a *neuromast*, consists of a group of sensory cells lying at the surface of the integument and accompanied by supporting cells (Fig. 671). Each sensory cell has a "hair" projecting from its exposed surface and is innervated by one of the terminal branches of a nerve fiber.



Fig. 671. Neuromast from the lateral line system of a dogfish. (After Johnson.)

Rheoreceptors are entirely absent in land vertebrates, but four general kinds have been recognized in fishes and aquatic amphibians, namely: (1) lateral-line organs; (2) scattered pit organs; (3) ampullae of Lorenzini; and (4) vesicles of Savi.

Neuromasts of the *lateral-line organs* tend to be arranged in rows extending from one end of the body to the other. In cyclostomes, some bony fishes, and all aquatic amphibians (including larval stages of anurans) they remain at the surface of the body. Usually, however, rows of neuromasts sink down to form grooves which then close over to form canals embedded in the skin but with numerous pores opening to the outside. In some cases, for example *Chimaera*, the grooves remain open. These canals have a fairly constant arrangement as seen in *Squalus* (Fig. 672). The *lateral-line canal* runs from the head to the posterior end of the body along the outer edge of the horizontal septum which divides epaxial musculature from hypaxial. In the head region there are three pairs of longitudinal canals: a *supraorbital* above the eye; an *infraorbital* below the eye; and a *hyomandibular* extending from the infraorbital posteriorly along the upper jaw region. There may also be

a small pair of *mandibular* canals on the lower jaw and a *supratemporal* over the top of the head connecting the two sides just posterior to the spiracle. The lateral line canals and the supratemporal are innervated by the vagus (Xth) nerve, except for a small part near their junction to which the *glossopharyngeal* (IXth) nerve goes. All the other canals are supplied by the *facial* (VIIth) nerve.

Scattered *pit organs* are isolated neuromasts, each sunk into a separate pit. In some fishes certain of these pits may be arranged in rows which occupy the same position as a groove or canal in another species.

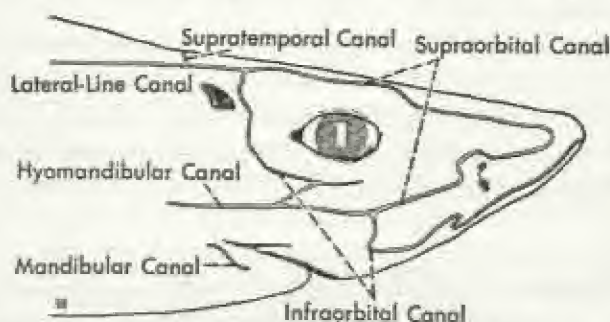


Fig. 672. Right-lateral view of the lateral-line system of the head of *Squalus*. (From Sayles, *Manual for Comparative Anatomy*, copyright 1938, by permission of The Macmillan Company, publishers.)

Whenever lateral fins are so placed that they would naturally extend over a portion of the lateral line, or by their movement cause an agitation in the water which would interfere with the reception of the stimulus produced by external currents of water, the part of the lateral-line canal interfered with may curve out of the way in a detour, thus avoiding interference (Fig. 673).

Various stages of elaboration of the lateral line may occur at the same time in different regions of the same fish, or at different times in the course of development. The eel, *Anguilla*, for example, during the early "leptocephalus stage," has only isolated pit organs present on the head region. Young fingerlings develop a lateral line closed anteriorly but open posteriorly, while the adult has the entire system insunken and closed except for craterlike pores along the line.

Among amphibians rheoreceptors are always present in larval and perenibranchiate forms, the lateral line being usually represented by three parallel rows of isolated clusters. Traces of these structures remain in some land amphibians in the form of spots on the skin, indicating the former locality of sensory clusters which have changed in function from rheoreceptors into tactile organs.

The *ampullae of Lorenzini*, as well as the *vesicles of Savi*, are highly modified pit organs that occur only in cartilaginous fishes. They are deeply sunken below the surface, the former enlarging into a bulblike cavity at the bottom of an elongated duct (Fig. 674), and the latter becoming entirely closed off from the outside. Both are equipped at the bottom with receptor cells, surrounded by abundant mucus, and terminating with sensory hairs.

The *vesicles of Savi* are found only in the aberrant electric fish, *Torpedo*, where they lie along the outer edge of the electric organ on either side, and around the border of the nasal pits. They are supplied by a branch of the trigeminal (Vth) nerve, but their function is unknown.

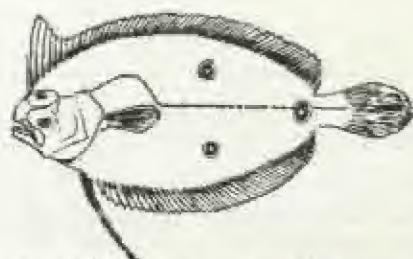


Fig. 673. A teleost fish, *Notosema*, showing a kink in the lateral line, which thus may avoid currents produced in the water by movements of the pectoral fin. (After Goode and Bean.)

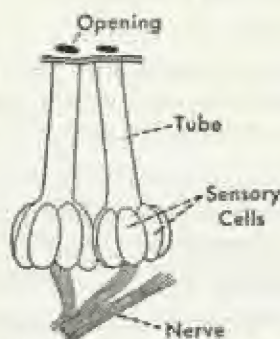


Fig. 674. Two organs of Lorenzini from a dogfish, *Scyllium*. (After Haller.)

The presence of abundant mucus in the lateral-line system and related pit organs led formerly to the idea that these organs were glandular and primarily secretory in function, but the discovery by Leydig in 1850 that they have a sensory rather than a motor nerve supply placed them definitely in the category of sense organs. Subsequent experimentation on fishes, by cutting different nerve supplies, showed that these sense organs make the animal receptive to coarse vibrations agitating the surrounding medium, as well as to the sustained impact of water in the form of currents. By means of such organs the fish is enabled to face against the water flow, even in darkness or in turbid waters when no "landmarks" are visible, and so to maintain its position without being constantly carried down-stream, or away with flowing tides and currents.

Rheoreceptors no doubt also help in making a fish aware of the approach of enemies which agitate the water by swimming movements, producing low vibrations that act as warning stimuli.

IV. CHEMICAL SENSE ORGANS

The chemical stimulation of taste and smell is brought about by contact with solutions of various substances. Liquids are tasted and gases are smelled. In order to taste a solid object it must first be reduced to liquid form. Even gases must be dissolved in a liquid before they can be smelled, since the delicate terminal hairs of olfactory receptors are effective only when surrounded by a lipoid film and by mucus or water in which odoriferous gases may be received.

The two sensations which we call smell and taste are served by at least ten or a dozen different kinds of receptors, each adequate for a particular distinct kind of stimulus.

Both of the groups of chemical receptors for tasting and for smelling are primarily located, like John Bunyan's lions before the gates of the Palace Beautiful, near the entrance of the digestive tract, where they pass upon the character of the entering food. While the nasal and mouth cavities in which these chemical receptors are for the most part located are not actually on the outside of the body, they are nevertheless integumentary invaginations and so, fundamentally, a part of the cutaneous system.

Tasting is necessarily always a matter of direct contact, but smelling, which makes an animal aware of odorous substances even at some distance away, has the wider range, since it serves not only as a food censor, but also directs locomotion in the quest for food, as well as localizing the presence of other animals. It plays a particularly important rôle in sexual allurement, especially in mammals whose glandular skin sends forth many characteristic odors.

Response to chemical stimuli in some of the simplest animals is not associated with definite receptors. For example, the chemical receptivity of *Paramecium* is confined to the anterior end of the body, while in *Stentor* it is diffused over the entire outside of the body. The sensitivity of sea-anemones to chemical stimuli is limited to the tentacles, while the outside of the columnar body is unresponsive to chemical stimuli but responsive to mechanical contact.

1. Olfactoreceptors

Moth collectors know that when a female moth is confined to a wire cage at night, males come from considerable distances and can easily be captured while fluttering around the cage, attracted by an odor scarcely perceptible to man, that emanates from the body of the imprisoned female. The antennae of the males in this case bear the receptors of smell.

There are antennal receptors for at least three different kinds of chemical stimuli also that have been demonstrated in certain ants. The presence of enemies, or ants from foreign colonies, is detected by receptors located on the 6th and 7th joints of the antennae. Nest mates having the same odoriferous password are recognized by receptors on the 8th and 9th antennal joints, while the odor of the nest itself is registered by receptors on the 12th joint.

Olfactoreceptors of vertebrates are definite neurons which, although morphologically simple and undifferentiated, have become physiologically diversified so that they are adequate for a considerable variety of different chemical stimuli.

The evolution of the olfactory apparatus in vertebrates shows it to have been originally a primary sense of first importance that has gradually been replaced in the course of phylogeny by other receptors. In the lower vertebrates the olfactory centers overshadow all the rest of the brain. Such animals live in an olfactory world. It is apparent that the earliest crawling land animals, snuffling around close to the ground among ferns and club mosses and other rank vegetation, had much less use for eyes than for an olfactory apparatus. Later on, with increasing emancipation from lowly ground life, and with the rise and dominance of the major senses of sight and hearing, the olfactory sense has taken more and more to the background, until, in the case of mankind, the sense of smell may be sacrificed with less inconvenience and regret than any other. It still plays a rôle in appetite and sentiment, however, although human experience and memory dwell upon sights and sounds rather than smells.

(a) **Odors.**—In the open air odors, or volatile substances, though rarely emanating in all directions equally as sound and light tend to do, are particularly influenced by air currents that may be present. The farther away odorous gases are from the point of release, the more diluted they become and the more slowly they disperse (Stephan's Law). Nevertheless extremely minute quantities of certain odors are perceptible at considerable distances from their origin, as every bloodhound attests.

Allison and Katz, in the *Journal for Industrial Engineering* for 1919, give a table in milligrams of minimum concentrations of various chemical substances that are perceptible to man in a liter of air. The quantity of chloroform is given as 3.3; iodoform, 0.018; propyl-mercaptan, 0.006; and artificial musk, which is by far the "smelliest" known substance that was tested, 0.00004 milligrams. No one of the above tested substances is encountered freely in nature.

The diffusion of odorous substances through water is very much slower than through air, yet in spite of this fact sharks are known to be able to

discover a dead body at considerable distance in a remarkably short time, although when cotton is stuffed into the nasal pits of a shark, it is unable to locate odorous food readily, even in the immediate neighborhood.

Land amphibians, reptiles, and carnivorous birds such as the vulture depend more upon the sight of moving prey than upon the sense of smell in finding food. There is a great variation among mammals. Rodents, ruminants, and carnivores, all of which have a highly developed olfactory sense, are said to *macrosmatic*. Many mammals, man for example, are *microsmatic*, that is, poor "smellers." Others are *anosmatic*, without any sense of smell at all, like cetaceans, whose nostrils have been readjusted into a periscopic position and are entirely devoted to respiratory uses.

Most evil smelling things are bad or poisonous, but not invariably so. Carbon monoxide gives out no olfactory warning although very poisonous, while certain famous cheeses, which are decidedly repulsive in odor, are not only non-poisonous but highly nutritious and beneficial.

The attempt to classify different odors objectively has not been very successful, although the existence of several specifically different kinds of olfactory receptors, adequate only for certain odors, is quite likely. Henning in 1916 proposed six different arbitrary categories of odors based upon their resemblance to well-known olfactory standards, namely, foul, flowery, fruity, burnt, spicy, and resinous.

(b) *Structure*.—Since smell, as contrasted with taste, has a much wider functional range, there is a greater elaboration of accessory structures in the olfactory apparatus than is necessary with organs of taste. There are not only

the olfactory neurons, but also skeletal capsules and cavities in which they are housed; various supplementary chambers or sinuses connecting with the olfactory cavities; devices for securing the passage of odorous substances across the receptors; and glands for maintaining a constant film of moisture over the exposed ends of the olfactory receptors.

The olfactory apparatus is the most anterior of all the sense organs. In man it appears first as a pair of ectodermal thickenings, which lie just in front of the developing medullary plate. By the third week of fetal existence they have become depressed into two nasal pits which are in close approximation to the olfactory lobes of the brain, and are brought into communication with the mouth cavity, both ontogenetically and phylogenetically, by a

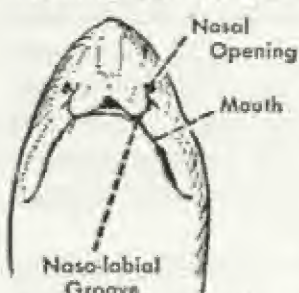


Fig. 675. Ventral view of the head of a dogfish, *Scyllium*, showing the naso-labial grooves. (After Schimkewitsch.)

channel, the *naso-labial groove* (Fig. 675), extending from the edge of each pit to the mouth.

In some fishes and amphibians the nasal passages are formed by the fusion of the edges of the naso-labial grooves. In man, however, the grooves fill in completely, the nasal pits push in considerably deeper, and from the posterior ends of the pits secondary openings break through into the mouth cavity. This process is completed by the end of the fifth fetal month. Failure of the proper closure of the naso-labial groove results in the deformity known as "hare-lip" (Fig. 676), although *shark-lip* would be a more appropriate term, since the cleft in the upper lip is not a single one in the middle as in hares but on either side as in sharks and other elasmobranchs.

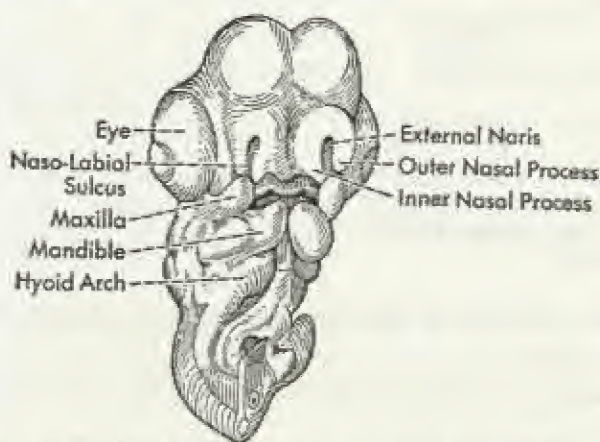


Fig. 676. Head of a chick embryo of 5½ days, showing the naso-labial sulcus, which would form a "hare-lip" if it remained open. (After Duval.)

The enlarged nasal cavity finally becomes differentiated into three regions, namely, vestibular, respiratory, and olfactory, distinguishable from each other by the character of the epithelium lining them.

The *vestibular region* is transitional between the skin on the outside and the mucous membrane within. It is characterized in mammals by the presence of sebaceous glands and by stiff outward-projecting, dust-arresting hairs, and forms that part of the nasal cavity which is principally under the protection of the projecting roof-like cartilaginous elements of the external nose, when such a structure is present, as in man.

Snouts have little to do with the olfactory sense but are rather associated with the tactile sense in nocturnal and burrowing forms, while in animals like pigs which "root for a living," they are mechanical organs of the first

order, strengthened sometimes by calcified cartilage. The trunk of an elephant, which is a combination of a long drawn-out nose and upper lip grown together, continues to perform the primary olfactory function, even though transformed into a grasping organ.

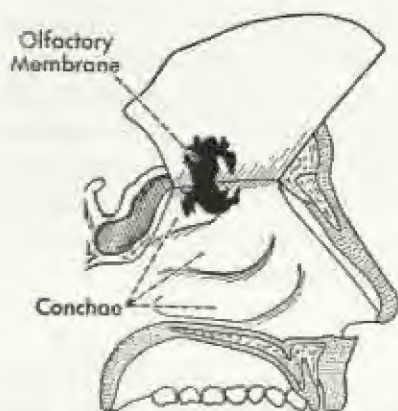


Fig. 677. Diagram showing the extent and position of the olfactory membrane in man. The nasal septum is represented as cut loose along its lower margin and swung upward. (After von Brunn.)

The *respiratory region* of the nasal chamber, the most extensive part of the olfactory mechanism, provides a place for the passage of air to and from the lungs. It has been described in Chapter XIII.

The so-called *olfactory region* is the innermost recess on either side of the nasal cavity (Fig. 677). In man it is comparatively small, the *olfactory membrane* being distinguishable by its yellowish brown pigmentation. Although the use of the pigment here is not definitely known, it has been demonstrated that albinos which lack it have a defective sense of smell.

The cellular units of the olfactory epithelium are of three kinds, namely, sustentacular, basal, and sensory. The numerous *sustentacular cells* are long slender supporting elements extending through the entire thickness of the

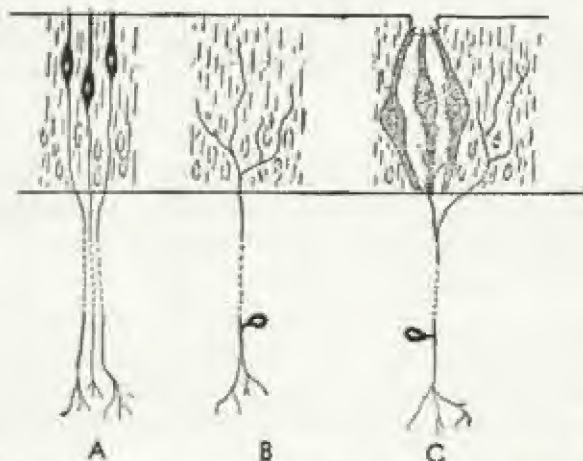


Fig. 678. Evolution of sensory neurons. A, primary sense cell from olfactory membrane; a, free nerve endings in epithelium, with nucleus of receptor neuron withdrawn from surface; c, secondary sense cells associated with nerve endings.

membrane. Between their slender inner ends are the *basal cells*. The *sensory*, or *olfactory*, cells are evenly distributed between the supporting cells. Each olfactory cell consists of a nuclear region from which a cylindrical process, comparable to a dendrite, extends to the surface where it terminates in several extremely delicate hair-like processes (Fig. 678). From the opposite end of the cell a slender neurite, covered by neurolemma but no myelin sheath, runs to the olfactory bulb of the brain. Many of these neurites together constitute the olfactory nerve, as described in the preceding chapter.

(c) **Accessory Parts.**—The circulation of water, containing dissolved gases, across the olfactory surface in the nasal pit of fishes, is effected largely by the presence of cilia. In elasmobranchs it is facilitated by a curving partition which partially subdivides each pit into intake and outgo regions. This division is carried further in many teleost fishes, as, for example, in the conger eel, *Muraena* (Fig. 679), in that each external naris has become double, thus presenting, instead of the two usual nasal openings, four chimney-like nostrils on the head, none of which penetrates to the mouth cavity.

With the establishment of the choanae and the transfer of air through the nasal cavities, a system of valves and muscles becomes elaborated in connection with nasal ventilation. (See Chapter XIII, Respiration.)

The remote situation of the olfactory membrane above the respiratory passage-way makes it possible ordinarily to breathe air without stimulating the olfactoreceptors to any great extent, even when odorous substances are about, unless air is drawn in vigorously over the upper olfactory route, as in "sniffing."

Animals primarily aquatic, such as fishes and amphibians, have the olfactory membrane spreading over the entire nasal cavity, but a differentiation into vestibulo-respiratory and olfactory regions is found in air-breathing amniotes, beginning with the reptiles. In animals secondarily aquatic, like seals and possibly whales, which have largely lost the olfactory epithelium, the nasal cavities become entirely respiratory in character.

Supplementing glands in the nasal passages that serve to provide an adequate degree of moisture are the lacrimal glands, the ducts of which at the inner angles of the eyes constantly drain down into the nasal chambers. This nasal flow of excess tears is particularly well demonstrated by a sniffing child emerging from an emotional crisis that results in weeping.

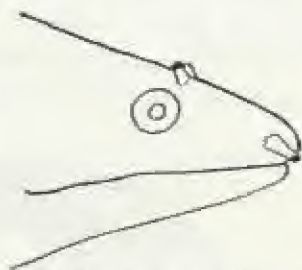


Fig. 679. Lateral outline of the head of a fish, *Muraena*, with projecting tubular nostrils that open into a common chamber but not into the mouth cavity. (After Wiedersheim.)

(d) **Evolution.**—The development of the nasal cavities in man finds a parallel in the evolution of these structures in the vertebrate series.

In general fishes have olfactory pits that are *culs-de-sac*, not extending down into the mouth cavity. The nasal pits of elasmobranchs, however, which are on the ventral side of the snout not far from the mouth, may connect with it by means of open naso-labial grooves (Fig. 675).

In dipnoans and more completely in amphibians the grooves of the pits become closed, thus establishing, in addition to *external nares*, or nasal openings, a pair of internal nares, or *choanae* (Fig. 251).

With the development in reptiles of a "hard palate," or secondary roof of the mouth, the passage-way between the external and internal nares becomes much elongated. With a choanal opening into the mouth it is possible to receive olfactory stimuli from the outside world, not only through the front door of the external nares but also by way of the back door of the choanae, by means of food substances taken into the oral cavity.

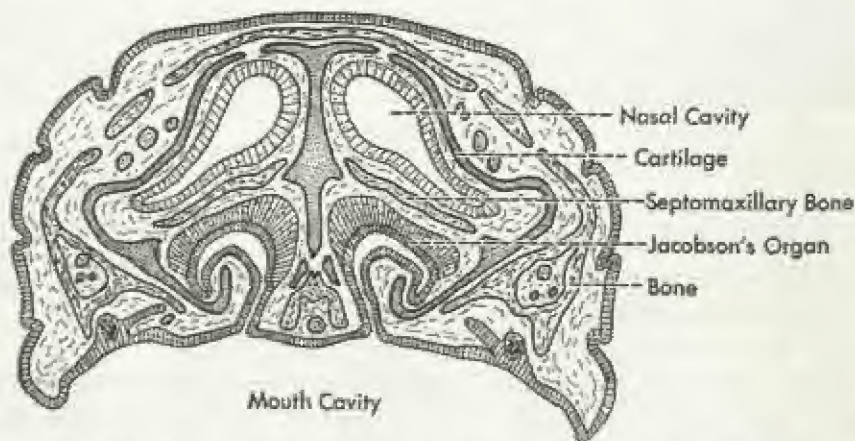


Fig. 680. Cross section through the head of a lizard, *Lacerta agilis*, with the lower jaw removed. Jacobson's organ is shown opening into the mouth cavity. (After Schimkewitsch.)

Animals that hold food in the mouth have an accessory structure, *Jacobson's organ*, which was first described in 1811. It is a cavity derived embryonically from the olfactory cavity and is lined with olfactory epithelium that is supplied by twigs from the olfactory (Ist) nerve and the trigeminal (Vth) nerve. In position it is ventro-medial to the nasal cavity on either side. Reaching its highest development in the snakes and lizards (Fig. 680), it is reduced in turtles and crocodiles and appears only as an embryonic structure in birds. It is present in amphibians although not opening into the

mouth cavity. Mammals show traces of Jacobson's organ embryonically, but in most instances it is a degenerate structure, its best manifestation being in monotremes, marsupials, insectivores, and rodents. It is entirely absent in whales, bats, and Old World monkeys. The history of Jacobson's organ in man is wholly intra-uterine. Arising at the beginning of the third month as small outpocketings of epithelium in the lower part of the nasal septum, it forms a slender blind sac on either side, reaching its greatest elaboration at about the fifth month. Before birth it becomes entirely reduced. This structure, which Kingsley refers to as "a kind of an olfactory organ," probably serves as an accessory olfactory apparatus for testing odorous substances held in the mouth.

The enlargement of surfaces for the exposure of epithelium within the nasal chambers is brought about in three ways: by the folding of the mucous membrane; by sinuses in communication with the main nasal cavities; and by *conchae*, or skeletal shelflike extensions of the nasal walls.

The method of membranous duplication is common among fishes. The mucous lining of the nasal pits of the dogfish, for example, bears a distant resemblance to the leaves of a book because of its numerous folds. Such a device would not be effective out of water, for the folds would tend to adhere together when not kept separate by immersion in an aqueous medium.

Reptiles have a single unrolled concha, or projection from the ectethmoidal wall of the nasal chamber on either side, which is slight in turtles, but of considerable size in crocodiles and alligators.

The nasal chamber of birds is compressed, in accordance with the general policy of compactness that characterizes avian anatomy. Its surfaces are compensatingly increased, however, by the presence of three conchae on either side, the most anterior of which is located in the vestibulo-respiratory region, while the smaller middle and posterior ones, that serve as supporting foundation for the olfactory membrane, are no doubt chiefly of value in supplying a moisture-producing surface for the respiratory mechanism.

Conchae reach their greatest elaboration in mammals, particularly ungulates, rodents, and carnivores, often becoming rolled like a scroll, thus presenting a maximum surface within a minimum space (Fig. 681). The nasal space in a sheep is larger than the brain cavity. In man, whose sense

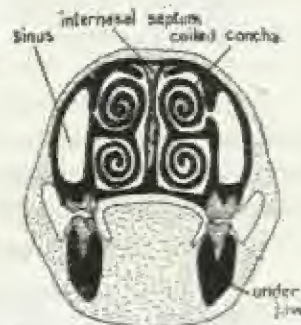


Fig. 681. Diagrammatic cross section through the nasal region of a mammalian head. (After Boas.)

of smell is much inferior to that of a truffle-hunting pig, the conchae are smaller in size and reduced in number to three (Fig. 677).

2. Gustoreceptors

Just as the chemical sense of smell is located with special reference to the entrance of the respiratory passages, so the sense of taste acts as a sentinel at the portal of the digestive tube, inspecting all substances that enter there.

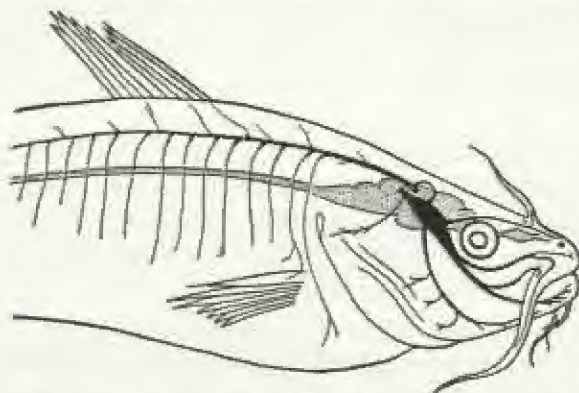


Fig. 682. Cutaneous gustatory branches of the facial nerve of *Ameiurus*. (After Herrick.)

(a) **Taste Buds.**—Gustoreceptors are composed of clusters of cells called *taste buds*, which follow the same plan throughout the vertebrate series, differing in the various groups principally in their arrangement with relation to different kinds of *papillae*, as well as in their distribution.

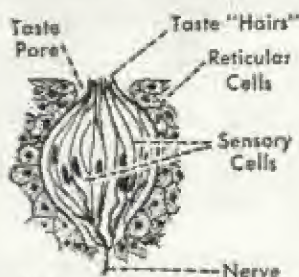


Fig. 683. A section through a taste bud. (After Burton-Opitz.)

The parent tissue that gives rise to taste buds is ectodermal in derivation. In many fishes, such as carp, sticklebacks, suckers, and catfishes, the ability to taste is not confined to the mouth cavity, but extends over the entire ectodermal covering of the body, even as far as the tail (Fig. 682). These external taste buds are supplied by the facial nerve. With emergence from water to land, gustoreceptors are withdrawn to the moist environment of the mouth cavity which is the logical place for encountering food solutions.

A typical taste bud (Fig. 683) consists of a compact group of receptor and sustentacular cells, the former of which are in contact with free nerve endings from cranial nerves. Each *sensory receptor cell*, which is slender and

elongate, terminates peripherally in a delicate protoplasmic "hair" which extends from the bud through the *taste pore*.

Taste buds are innervated by the facial (VIIth), glossopharyngeal (IXth), and vagus (Xth) nerves. The facial supplies the anterior part of the mouth cavity, including the anterior two-thirds of the tongue with its fungiform papillae in mammals. The glossopharyngeal supplies the posterior part of the mouth cavity, including the posterior third of the tongue with its vallate and foliate papillae in mammals. The vagus supplies the pharynx, including the taste buds of the epiglottis in mammals.

Although taste buds occur in various parts of the mucous membrane of the mouth and pharynx, they are especially abundant on the papillae of the tongue (Fig. 237).

(b) **Comparative Anatomy.**—Amphioxus has cellular structures that resemble taste buds upon the cirri around the mouth, but their function is unknown.

The sense of taste in fishes is, as already pointed out, much more generalized than in land forms, the gustoreceptors extending over the outside of the body where they appear more as free endings than as taste buds.

Not much is known of the sense of taste in amphibians, but these animals do possess nerve endings in the skin that serve as chemical irritoreceptors. They have groups of cutaneous cells also which are probably more tactile than chemical in function. Whatever sense organs may be found in the amphibian mouth have slight opportunity to be of gustatory service, since the food is swallowed at once without being held in the mouth.

In reptiles, particularly crocodiles and snakes, taste buds are located in the posterior part of the mouth cavity, which is less cornified than the anterior part.

Taste buds are present but scarce in the bird's mouth, and are likewise situated posteriorly instead of on lingual papillae as in mammals. The majority of birds with small cornified tongues have most of the taste buds in the floor of the mouth, while birds like parrots, with large fleshy tongues, give lodgment to the gustatory organs on the tongue itself, or along the sides of the maxillary half of the beak.

Taste buds reach their greatest development in mammals, such as ruminants, that have specialized grinding molars and retain forage within the mouth cavity for a prolonged period before consigning it to the absorptive part of the digestive tract. The taste buds are not confined solely to the tongue, but are found also on the ventral surface of the soft palate, on the epiglottis, on the pharyngeal wall, and even on the inside surfaces of the cheeks.

The number of taste buds to each vallate papilla varies greatly in different mammals. Hesse has estimated that sheep have 480; cows, 1760; and pigs, 4760. A cow, having about 20 papillae, would consequently possess approximately 35,000 taste buds, while a giraffe, which is known to have over 30 papillae, would probably prove to be still more generously endowed.

Stahr has made the interesting observation that taste buds on the tongue of the domesticated white rat are considerably reduced in number as compared with those of the wild rat that works for a living.

In man there is an oval area on the dorsal surface of the tongue that is free from taste buds, as is also the under side of the tongue (Fig. 684). That the sense of taste in man is degenerating is proved not only by the fact that taste buds are more widely distributed during the fifth to the seventh months of fetal life than in the adult, but also by the fact that the inner surfaces of the cheeks respond to taste far more keenly in children than in older persons.

(c) **Classification.**—The subjective classification of gustatory sensations into pleasant, unpleasant, indifferent, or absent is better replaced by an objective grouping according to the types of gustatory stimuli. Four such categories may be accepted as demonstrable, namely, sweet, salty, sour, and

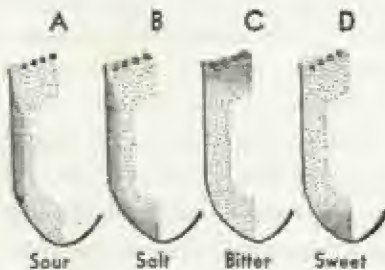


Fig. 684. Diagrams of the right half of the human tongue, illustrating the distribution of the taste buds. The dots represent the area and concentration of a given sense of taste. A, the sour taste, concentrated on the edge; B, the saline taste, at the tip and on the edge; C, the bitter taste, at the base; D, the sweet taste, at the tip. (Modified from Hänig, after Parker.)

bitter. Intergrades probably occur, and there is no doubt that confusion often results, particularly with olfactory and tactile stimuli. Thus when one speaks of a "slimy" or a "gritty" taste, he is referring in reality to tactile stimulation, while the so-called "taste" of onions, wine, coffee, tobacco, tea, fruits, and spices is largely a matter of olfactory stimulation. Most "flavors" which are commonly associated with the sense of taste arise largely from olfactory stimuli, as is realized when with a "head cold" the swollen mucous membranes largely occlude the choanal passages and food "loses its taste."

Although indistinguishable from each other histologically, there are specific gustoreceptors, adequate for each of the four kinds of stimuli just mentioned, since, upon application of cocaine to the tongue the sense of bitter disappears first, then those of sweet, salty, and sour in succession.

The distribution of the four kinds of receptors over the surface of the

human tongue has been carefully mapped (Fig. 684), thus demonstrating that the receptors of gustation are different. It will be seen that sour receptors predominate along the edge of the tongue; salty, both at the tip and at the sides; bitter, at the base; and sweet, at the tip.

Extensive tests by Blakeslee and others with phenyl-thiocarbamide, a harmless substance which tastes bitter to most people, reveal the fact that all human beings are not equipped with the same array of gustoreceptors. Out of 2550 individuals tested in one series of experiments 65.5 per cent reported the substance as bitter; 28.0 per cent, tasteless; 2.3 per cent, sour; and 4.2 per cent, some other taste. It is obvious that all people do not interpret the same chemical world the same way, because of a difference in their gustoreceptors.

3. Irritoreceptors

The moist skin of amphibians and fishes is sensitive to certain chemical stimuli that act as irritants. In reptiles, birds, and mammals, whose integument is adapted to conditions in dry air, the stimulus produced by common chemical irritation aside from that interpreted as taste or smell is confined mostly to moist mucous surfaces. Here it may be very noticeable, as when a whiff of ammonia causes "watering of the eyes" or choking reflexes. These are stimuli transferred to the brain by the pathway of the fifth cranial nerve, instead of the first, and the receptors may properly be termed irritoreceptors rather than olfactoreceptors.

Irritoreceptors are closely related to those of contact and pain, but are nevertheless distinct from them, as is demonstrated by the fact that cocaine differentiates them from each other, and also because they do not become simultaneously exhausted upon rapidly repeated stimulation. Parker has shown that the tail of amphioxus, for instance, after it no longer responds to the application of weak nitric acid, is still fully responsive to the touch of a camel's-hair brush. Cole has also demonstrated that a frog, anaesthetized by a one per cent solution of cocaine to the point at which it is entirely oblivious to the mechanical stimulation of pinching or scratching, will still respond vigorously to the application of a salt solution.

"We are, therefore, entirely justified," says Parker, "in concluding that the common chemical sense is a true sense with an important set of receptors and a sensation quality entirely its own."

By experiments of elimination it has been shown that irritoreceptors are free nerve endings with spinal or cranial connections, whose distribution is confined to the skin of aquatic vertebrates, or to the moist cutaneous surfaces of land forms.

V. GRAVITY ORGANS

1. Equilibrium

Although equilibration and hearing are two quite distinct functions, the sense organs concerned have much in common in vertebrates and are often described as *stato-acoustic organs*. The same is not true of invertebrates generally, since in them the sense organs regulating equilibrium, when present, are distinct and independent of those receiving sound waves.

The function of equilibrium is unnecessary and absent in plant-like stationary animals, like hydroids and corals that remain attached in one position, although stationary plants possess devices which are comparable to gravity receptors, enabling stems and roots to assume a position, positive or negative, with reference to the center of the earth.

This response, *geotaxis*, is not fundamentally different from equilibration in moving animals, that maintain their bodies by their own efforts in various positions with reference to gravity. Geotaxis is brought about by the arrangement of the component parts within the responsive cells, the heavier parts "settling" to the bottom of the growing geotactic cells, thereby orienting them.

There are three general types of equilibrium, namely, indifferent, stable, and labile.

Indifferent equilibrium is uncommon and involves no specific receptors. It may be seen, for example, in the heliozoans, which are spherical microscopic protozoans that hang suspended any side up without contact with solid objects, and also in the green globular colonies of *Volvox*, which roll about in pond water without definite orientation to gravity.

Stable equilibrium, that likewise is not dependent upon special sense organs, applies not only to inert forms but also to living bodies, such as a flounder that comes to rest on one side, like a bicycle laid flat upon the ground. In this case the pull of gravity allows the animal to come to rest without individual muscular effort.

When, however, the center of gravity is too high to allow balancing without muscular effort, like a dog "standing on all fours," or a man balanced upon two legs, then *labile equilibrium* is demonstrated.

This latter type involves biological factors within the body, as well as the physical pull of gravity from without, for not only must a tension be maintained between opposing muscles to prevent collapse, but a coördinating nervous apparatus, including sense receptors, is also necessary to mediate between the body of an organism and the environmental setting in which it finds itself.

2. Statoreceptors

In lower free-swimming animals the sense organs of equilibrium are usually *statoreceptors* of some sort, depending for their action upon differences in the pressure of a comparatively heavy secreted mass, the *statolith*, which is brought into contact with surrounding sensory receptor cells whenever there is a change in the position of the body.

Around the margin of a floating jellyfish at the base of the tentacles that hang like a fringe from the edge of the "bell," there may be arranged a row of *statocysts*, each consisting of a hollow chamber lined with sensitive cells and containing a pendulous "clapper," which is made heavy by the deposition of limy salts in its end (Fig. 685). Whenever these fragile medusae in the course of their aimless voyagings upon the surface of the ocean are tipped up at an unusual angle by the force of the waves or by any other outside agency, the tiny loaded clappers within the statocysts swing over and bump the sensory cells that are on one particular side, with the result that the jellyfish rights itself sufficiently to bring the swinging clappers to a standstill, thus restoring equilibrium.

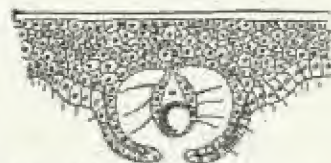


Fig. 685. Statocyst of a medusa, *Rhopalonema*, consisting of a weighted "clapper," supplied with sensitive "hairs," within a sensory bell. (After Hertwig.)

If the statocysts half way around the margin of a jellyfish are carefully dissected off or destroyed in any way, the animal is no longer able to right itself, but floats about in an unnatural attitude in the water. Anyone who has ever heard the clang of a bell-buoy and seen it rock back and forth when the surrounding water is agitated can understand perfectly the way the statoreceptors of jellyfishes operate.

Equilibratory mechanisms, presenting various modifications embodying this fundamental idea, occur both in free-swimming coelenterates and arthropods, as well as in various other invertebrates.

Among vertebrates the function of equilibration is accomplished not so much by static organs alone, as through the cooperation of several sense organs, primarily devoted to other purposes.

Thus a man maintains his upright posture without collapsing through the interaction of (1) tangoreceptors upon the soles of the feet that are in contact with the ground, acting as thigmotactic pressure organs; (2) the sense of sight, which informs and reassures him of his relation to his surroundings; (3) the proprioceptive "muscle sense," that attends to the proper tension of the opposing muscles; and finally (4) nerve endings from the

acoustic (VIIIth) nerve, connecting with the semicircular canals of the ears, which have a gravity function much like that of the statoreceptors of the invertebrates.

If for any reason any one of these four factors is withdrawn, equilibrium is either upset or maintained with difficulty, as anyone may observe by watching a young child that is learning to navigate a toppling body upon wobbly legs.

3. Semicircular Canals

The semicircular canals are embryologically inseparable from the hearing portions of the vertebrate ear. Further the essential sensory cells of both parts of the ear are so-called "hair-cells" comparable to those which are found in neuromasts. Consequently all of these parts may be grouped together as the acoustico-lateral system.

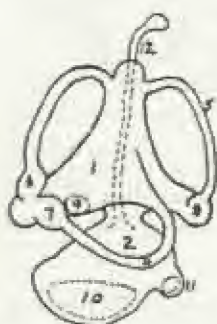


Fig. 686. Diagram of the left membranous labyrinth of a vertebrate ear. 1, utricle; 2 saccule; 3 4, 5, the semicircular canals with their ampullae (6, 7, 8); 9, macula utriculi; 10, macula sacculi; 11, macula lagenae; 12, endolymphatic duct. (After Wiedersheim.)

As the origin and arrangement of the semicircular canals will be more fully considered in connection with phonoreceptors, it is only necessary to point out here that they are typically three in number on each side of the body and are placed approximately at right angles to each other in the three planes of space (Fig. 686). Near one end of each fluid-filled canal there is an enlargement, or *ampulla*. The ampullae are static sense organs, responding to the stimulus of differential pressure. In order that the body movements may not upset these biological seismographs, they are buried deep in the temporal bone, which is the densest bone of the skull.

A group of delicate receptor cells, bearing stiff hairs, projects into the fluid-filled cavity of the ampulla (Fig. 687) and connects with the vestibular branch of the VIIIth nerve, forming a device which receives stimuli from the movement of the fluid (*endolymph*) contained within the tube, whenever the apparatus is tipped into a new position. Each of these sensory areas is known as a *crista ampullaris*.

Since the semicircular canals occupy three different planes, the combined stimuli received by the three ampullae make it possible to detect any shift in position, thereby initiating muscular responses appropriate for the maintenance of equilibrium.

Otoconia, which are usually either crystals or concretions of calcium

salts, may be secreted in the ampullae and become attached to the projecting hairs of the receptor cells, especially in land vertebrates. In selachians sand grains, instead of tiny concretions, serve as the otoconia.

Within the statoreceptor apparatus of the ear of most fishes the limy concretions may acquire considerable size and solidity, when they become known as *otoliths*, or "lucky bones" of fishermen. These otoliths are used to determine the approximate age of individual fishes, since they show lines of growth, resembling the rings of growth in the woody trunk of a tree.

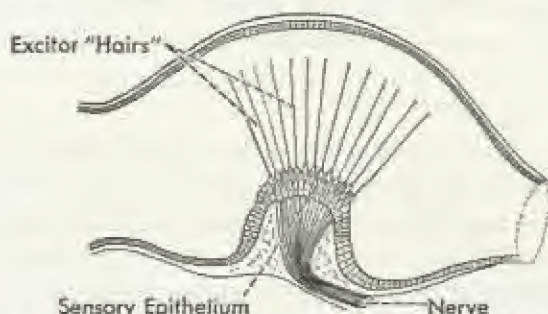


Fig. 687. Long section through an ampulla of the ear of a fish, *Gobius*. (After Hensen.)

The statoreceptor mechanism of the semicircular canals does not present any great amount of variation throughout the vertebrate series, except in cyclostomes. The hagfish, *Myxine*, equipped with a single semicircular canal bearing an ampulla at each end, and the lamprey, *Petromyzon*, with two canals, the third one being missing, can no more sense a three-dimensional world than we, with three canals, can understand the "fourth dimension."

The abnormal semicircular canal system of cyclostomes is probably more a degenerate than a primitive system, dependent upon the semi-attached habit of these parasitic vertebrates.

The peculiar erratic circling movements that are characteristic of Japanese waltzing mice are correlated with defective statoreceptive organs, or semicircular canals.

4. Weber's Organ

A problematical structure called *Weber's organ* is found in connection with the stato-acoustic apparatus in the ear of certain fishes. The two internal ears become connected by a transverse canal from which a row of small ossicles extends to the anterior end of the swim bladder. This connection, known as Weber's organ, is said to transmit movements of the anterior wall of the swim bladder to the ear. Its real function is unknown.

VI. PHONORECEPTORS

Hearing consists in the reception and interpretation of stimuli caused by vibrations of material particles. For this purpose the auditory sense organs have been evolved, first among lower forms that are submerged in water. Later, after emergence into the rarer medium of air, these organs become of greater importance.

In fishes the lateral-line organs, or rheoreceptors already mentioned, take the place to a considerable extent of organs of hearing, since currents produced by moving water and disturbances of slow vibrations rather than "sounds" are the most important environmental changes to dwellers in the silent aquatic world.

No doubt to many transitional thigmotactic animals, particularly to amphibians whose bodies are not yet elevated from major contact with solid earth by means of supporting legs, the vibrations which are of the greatest service and for which their sense organs are especially adapted are seismic rather than auditory in character. It is mostly, however, vibrations which pass through the air that are concerned with the true sense organs of hearing. In this rarer medium, through which sound waves pass more slowly and with less intensity than through the denser media of water and earth, it becomes the task of evolution to elaborate intensifying and collecting devices of various sorts to supplement the sensory auditory receptors.

It has thus come about that the auditory apparatus of the higher land vertebrates consists not only of a sensory receiving apparatus, the *internal ear*, but also of a *middle* and an *external ear*, whose supplementary functions are primarily the collection and amplification of vibrations from the air.

Of these three pairs of "ears," the internal ears alone are essential and present in all vertebrates that hear. In amphibians the middle pair of ears is added, although it is incorrect to speak of a "middle ear" until the external ear, which begins with reptiles and reaches its highest elaboration in mammals, is developed.

In describing the vertebrate ear it may be well to consider the simpler accessory parts first, and the more complicated and essential parts of the internal ear last, following the path taken by sound vibrations as they go to the nervous system of the listening animal.

1. The External Ear

The external ear of the higher vertebrates consists of a projecting flap, the *pinna*, which is furnished with *muscles*, and an *auditory canal*. The

pinna, a mammalian acquisition, is a peculiarly molded, flat, skin-covered, elastic cartilage in man with a cuplike *concha*, in the center, surrounding the entrance into the auditory canal. This opening is guarded on either side by two projections, the *tragus*, and *antitragus* (Fig. 688). The lower end, or *lobule* of the human ear, is fleshy, pendulous, and without cartilaginous support. In a considerable percentage of human kind the lobule is absent, or at least not free from the side of the head. The upper curving edge, or *helix*, of the pinna often presents an appearance suggesting animal ancestors (Fig. 689). When unrolled at the upper margin and more or less pointed, it is known as the "satyr ear," such as was possessed by Donatello in Hawthorne's famous story of *The Marble Faun*. If the projecting part is folded inward it makes the so-called "Darwin's point," more often seen in human males than females and quite characteristic of monkeys and apes. Embryonically the pinna passes through the satyr stage before attaining its final characteristically human outline.

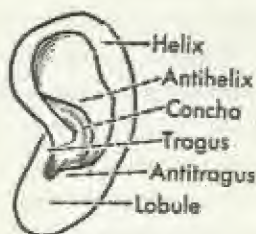


Fig. 688. Pinna of a human ear. (After Cunningham.)

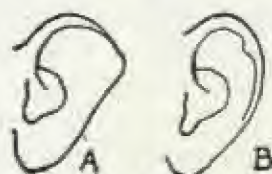


Fig. 689. Outlines of two ears A, monkey, *Macacus*; B, a human pinna, showing "Darwin's point," which is an infolding that resembles the projection on the pinna of the monkey's ear. (After Schwalbe.)

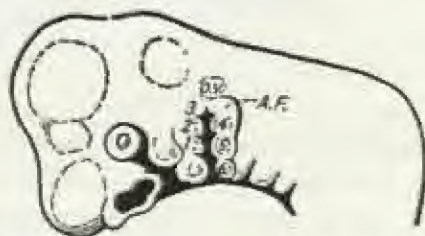


Fig. 690. Embryonic stages in the development of the pinna. 1, tragus; 2, 3, helix; 4, 5, antihelix; 6, antitragus; 1, 2, 3, elevations of mandibular arch; 4, 5, 6, elevations of hyoid arch; A.F., auricular fold; o.v., otic vesicle. (After Arey.)

The pinna develops on either side of the spiracular cleft which becomes the locus of the auditory canal. It arises originally as six knoblike elevations, three of which are borne by the mandibular, and three by the hyoid arch (Fig. 690).

Pinnae become degenerate in aquatic and burrowing animals, such as seals, gophers, and moles, where they would serve no good purpose and might even be a disadvantage, but they are large in animals like bats that

are active at night or in twilight, as well as in fast runners of open spaces, such as deer, hares, kangaroos, and antelopes. Also in arboreal animals, like squirrels, whose eyes are protected to a certain extent by the ears from chance encounters with twigs and branches, they are generous in size.

Spallanzani (1729-1799) long ago discovered that a bat, even after it had been blinded, was still able to avoid a maze of strings stretched across a chamber. The result of this classical experiment is not so much to be wondered at when it is remembered that bats are naturally active at twilight, a time when dependence upon sight in avoiding obstacles and in encountering insect prey upon the wing is of much lessened importance. It has recently been shown that these crepuscular animals ordinarily emit 20-60 supersonic screeches per second while in flight. The supersonic waves, which are audible to bats although above the range of the human ear, are reflected by even such slender objects as strings. Large external ears enable the bats to pick up the echoes of their voices and thus to avoid obstacles. Detection of objects by a system of reflected high-frequency waves thus long antedates man's use of radar.

In most animals pinnae aid in catching the *direction* whence sound waves come. A deaf person sometimes supplements this function of the pinna by cupping the ear with the hand.

Many animals have pinnae that are movably hinged to the skull and supplied with muscles, so that they may be easily directed to detect the source of sounds without the inconvenience of turning a heavy head.

The *ear muscles* are under the control of the will. They are of two kinds, *intrinsic* within the pinna itself, and *extrinsic*, connecting the pinna with the skull, thus effecting the movement of the external ears (Fig. 591).

In many breeds of domestic animals, as for example, pigs, sheep, goats, dogs, and rabbits, "lop ears" develop that lack much of muscular control as contrasted with upright hinged pinnae. In the security that comes with long domestication these animals have lost something of the habitual alertness that is the salvation of wild animals. Elephants are perhaps the only wild forms with pendulous non-erectile ears, but the self-confidence that goes with dominant size no doubt makes the direction from which hostile noises come a matter of comparative indifference to them.

In mammals the *external auditory canal* is the passage-way that leads to the middle ear. It is about 2.5 centimeters long in man, slightly bent and larger at either end than in the middle. For the external third of its length its walls are kept rigid by cartilage, continuous with that of the pinna, while for the remainder of the way into the skull the walls become bony, forming a projecting tube from the temporal bone.

The auditory canal is lined with skin, and is supplied with *wax glands* and outward-projecting *hairs*, both of which are devices that serve not only as dust-arresters, but also for the discouragement of crawling and flying insect explorers.

2. The Middle Ear

A *middle ear*, or *tympanum*, in the form of an irregular air-filled chamber, is hollowed out of each temporal bone between the external auditory canal and the internal ear.

A deep attic-like dorsal recess, the *epitympanum*, communicates with mastoid "cells," or spongy cavities, in the blunt mastoid process of the temporal bone (Fig. 514). Below, the *Eustachian tube* opens into the nasopharynx (Figs. 691 and 692).

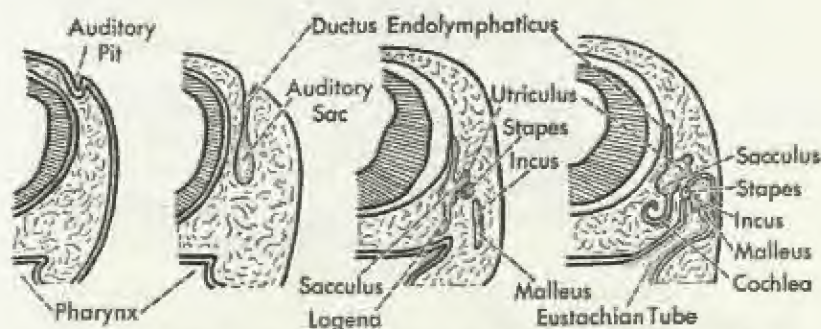


Fig. 691. Diagrams of stages in the development of the ear. (After Brandt.)

Across the inner end of the auditory canal and separating it from the middle ear is the "ear drum," or *external tympanic membrane*, which is attached in a groove, the *tympanic sulcus*. In man it is about 1 mm thick and 10 mm in diameter, being slightly thicker in the center than around the margin. It is set obliquely across the passage-way, and thus a larger ear drum with a greater expanse of surface is exposed to the impact of vibrations than would be possible if it extended squarely across at right angles to the auditory canal. The ear drum is relatively nearer the surface in a child than in an adult, while a newly born infant is temporarily deaf until the collapsed tympanic cavities are filled with air by way of the Eustachian tubes, following the effort that accompanies the first protesting cries with which it greets the world. These "first cries" of the newly born have been called the most joyful sounds in all nature, for they assure the anxious listeners that the

young stranger is a going concern, having marvelously made the critical transition from uterine existence to citizenship in the world.

On the face of the tympanic wall opposite the ear drum and next to the inner ear, are two windows, the *fenestra ovalis* and the *fenestra rotunda*, similarly curtained by drumhead-like membranes, so that the middle ear bears some resemblance to a hollow drum with very small membranous heads at the two ends (Fig. 692).

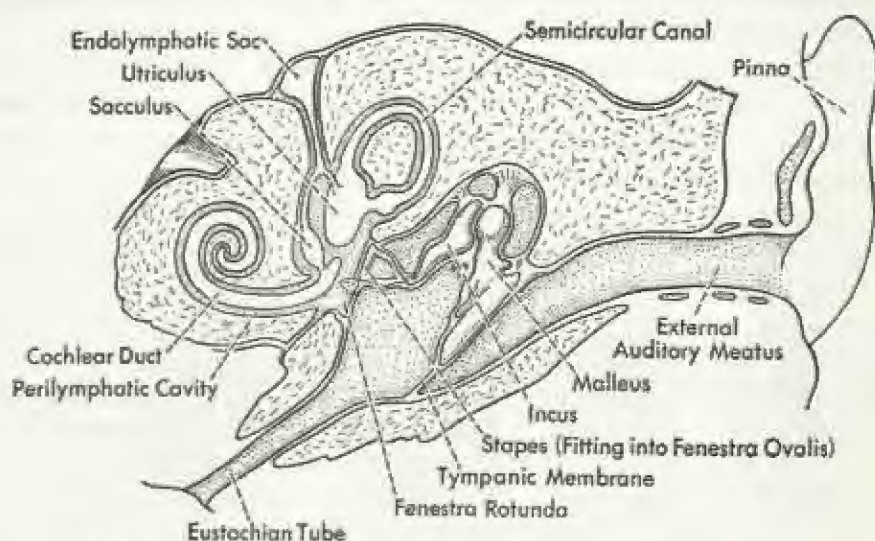


Fig. 692. Diagram of the ear region of an adult mammal. (After Goodrich.)

The *tympanic cavity*, or middle ear, in land forms is derived from the inner part of the ancestral spiracular cleft of the elasmobranch fishes that lies between the mandibular and hyoid arches of the primitive splanchnocraniums. In forming the middle ear the pharyngeal pouch never breaks through to the outside. The intervening "skin" remaining at the outer end of the spiracular pharyngeal pouch becomes the external tympanic membrane, while the opposite end extends to the pharynx as the Eustachian tube. Thus the external tympanic membrane is made up of an ectodermal layer on the outside and an endodermal layer on the inside.

The *Eustachian tube* is a ventilator of the tympanic cavity. Broader at the pharyngeal than at the tympanic end, it remains closed except during the act of swallowing when it may open sufficiently to permit an adjustment of air within the tympanic cavity. When the pressure of air is so adjusted that it is the same on the inside of the tympanic membrane as on the outside,

the membrane is thus made free to vibrate slightly back and forth in response to the impact of sound waves. When one enters a tunnel in which the pressure of the air is above that of the atmosphere outside, the ear drum is pressed slightly inward and, like a bellying sail in a stiff breeze, does not vibrate. To relieve the sense of pressure in the ears, when it occurs, it is only necessary to swallow, thus admitting more air through the Eustachian tube into the middle ear chamber.

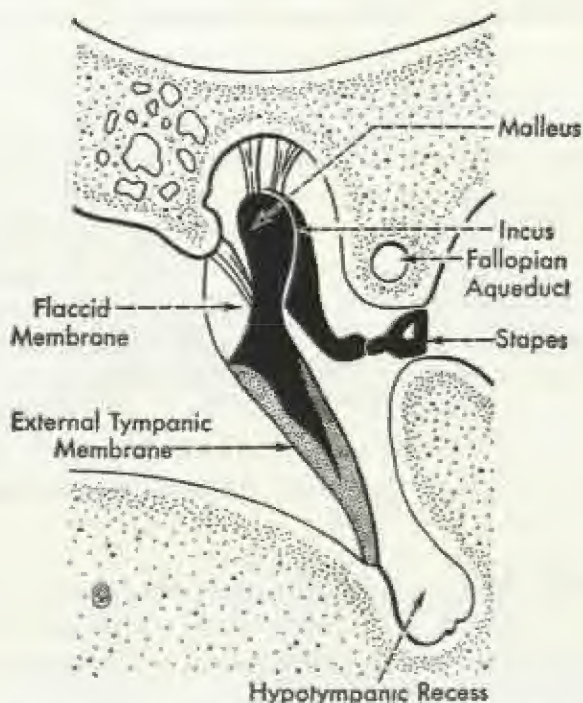


Fig. 693. Ear bones within the tympanic cavity. (After Rouvière.)

Sound waves which impinge upon the tympanic membrane are handed across the tympanic cavity to the inner ear, intensified and with their amplitude reduced during the passage, by means of a chain of three tiny ear bones, the "hammer," *malleus*; the "anvil," *incus*; and the "stirrup," *stapes* (Fig. 693).

The malleus is attached to the inner face of the ear drum by its "handle," while the stapes, which is articulated to it by means of the intervening incus, fits into the membrane stretched across the fenestra ovalis and, somewhat like the plunger of a piston, transfers by a thrust to the inner ear the sound vibrations which strike the drum.

In amphibians, instead of a chain of three bones, there is a single rodlike *columella*, extending from the ear drum directly to the fenestra ovalis (Fig. 694A). This device forwards vibrations from the drum to the inner ear with equal power and amplitude, instead of with an increased thrust and lessened amplitude as is the case with the chain of ear bones in mammals.

There may be two parts to the columella in reptiles and birds, either jointed or fused with each other (Fig. 694B). The inner element, which is homologous with the stapes of mammals, is the *plectrum*, while the outer part close to the drum is called the *extra-columella*.

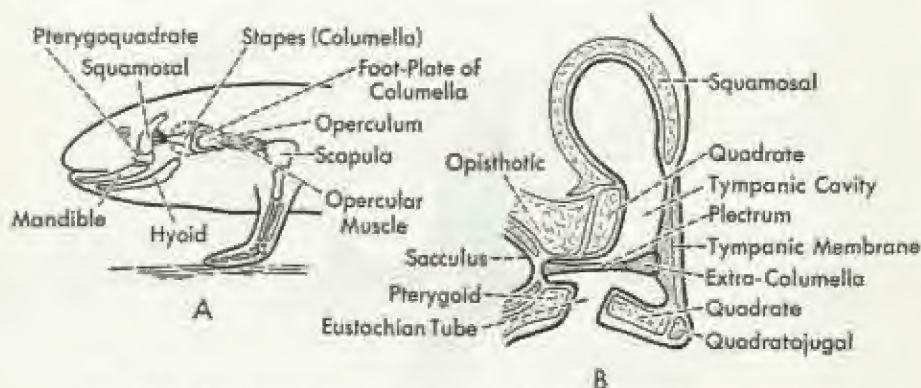


Fig. 694. Ear bones of urodeles (A) and turtles (B). (A, after Kingsbury and Reed; B, after Plate.)

In monotremes and marsupials the stapes remains cylindrical and solid at the enlarged inner end, like a pestle, but in other mammals it is pierced by a hole through which a blood vessel passes, so that it takes on a fancied resemblance to a stirrup, hence its name.

Two tiny muscles lie within the tympanic cavity. The *tensor tympani*, attached to the malleus and supplied from the VIIth cranial nerve, regulates the tension of the tympanic membrane. The *stapedius*, which is fastened to the stapes and supplied from the Vth cranial nerve, adjusts the fitting of the stapes in the fenestra ovalis.

The ear bones have a dramatic origin, being made over from skeletal elements of the splanchnocranium that formerly were put to quite different uses. The amphibian columella corresponds to the *hyomandibular element* of fishes, that is, to the most dorsal part of the hyoid arch. The inner end of the columella is homologous with the stapes of the mammalian ear, while the malleus and incus, which are peculiar to mammals, are derived from the *articular bone* of the primitive lower jaw, and the *quadrate bone* of the

original upper jaw respectively (Table VII). Thus mammals may be said to hear through the jaw bones of their phylogenetic ancestors.

3. The Internal Ear

The baffling internal ear, buried in the dense temporal bone, is made up of extremely delicate cells surrounded in life by fluids. It is a very difficult structure to dissect, and consequently histological sections, owing to different technics employed in their preparation with the inevitable distortion that results, have not always presented a dependable picture of the truth. Nevertheless essential agreement about many details has been gained.

The internal ear, which contains the essential phonoreceptors, is a closed ectodermal sac, the *membranous labyrinth*, peculiarly molded and called a "labyrinth" on account of its complicated structure (Fig. 686). It is filled with a fluid known as *endolymph* and is surrounded by a *bony labyrinth* in the form of a case hollowed out of the petrosal part of the temporal bone, conforming intimately to the contours of the membranous labyrinth. For the most part the membranous labyrinth does not adhere closely to the bony labyrinth but is separated from it by a space filled with *perilymph*.

(a) **Development of the Membranous Labyrinth.**—The inner ear, being primarily a static organ, is placed at the anterior end of the system of lateral-line organs and is probably derived from it. Like the pits of the lateral-line organs the membranous labyrinth of the ear is first of all an ectodermal

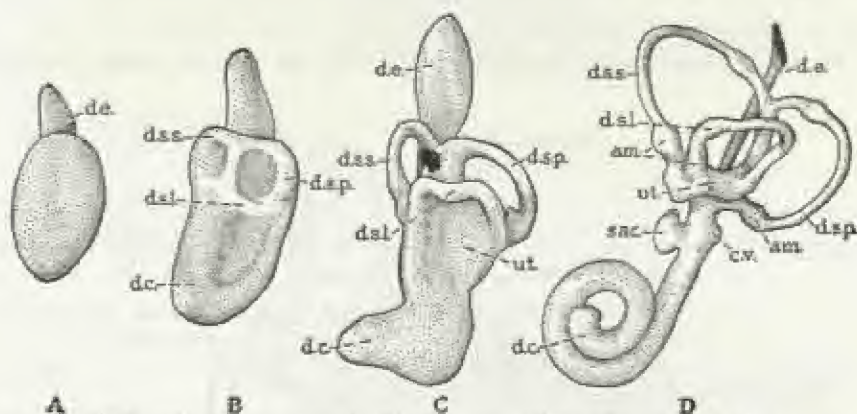


Fig. 695. Four stages in the development of the human membranous labyrinth, as seen in lateral views of the left ear. *am*, ampulla; *cv*, vestibular caecum of *d.c.*, cochlear duct; *d.e.*, endolymphatic duct; *d.s.l.*, *d.s.p.*, and *d.s.s.*, horizontal, posterior, and anterior semicircular canals; *sac*, sacculus; *ut*, utriculus. (From Bremer and Weatherford, *Lewis and Stöhr's Histology*, copyright 1944, by permission of P. Blakiston's Son and Company, publishers. After Hia, Jr.)

invagination, appearing as an isolated vesicle on either side of the head about opposite the anterior end of the myelencephalon. As it sinks below the surface it leaves an *invagination canal*, which at first remains open to the outside but later is closed off, thus making the vesicle of the future inner ear a completely closed sac surrounded by mesodermal tissues (Fig. 695).

By constriction this sac is next marked off into a dorsal *utriculus* and a ventral *sacculus*. At three points in the utricular region the walls become pinched together into flattened, semicircular folds placed approximately at right angles to one another. By this pinching process the two walls of each of these flattened folds come into contact with each other except along its curved outer edge. Thus along the outer margin of each fold there is formed a semicircular canal, opening at either end into the main part of the utriculus. Absorption of the central parts of the folds leaves behind the three loops of the *semicircular canals* without destroying the continuity of the general cavity within the sac or allowing the sac to break through to the outside.

Meanwhile the sacculus sends out a *cochlear sac* which eventually elongates and coils to form the *cochlear duct* with an auditory rather than a static function.

(b) **Structure in Mammals.**—For the most part the membranous labyrinth lies suspended in the perilymph, being held in place by strands of connective tissue which extend from it to the periosteal lining of the bony labyrinth. In the cochlear region, however, parts of the duct are in direct contact with its bony envelope.

In each membranous labyrinth there are six sensory areas: a *crista*

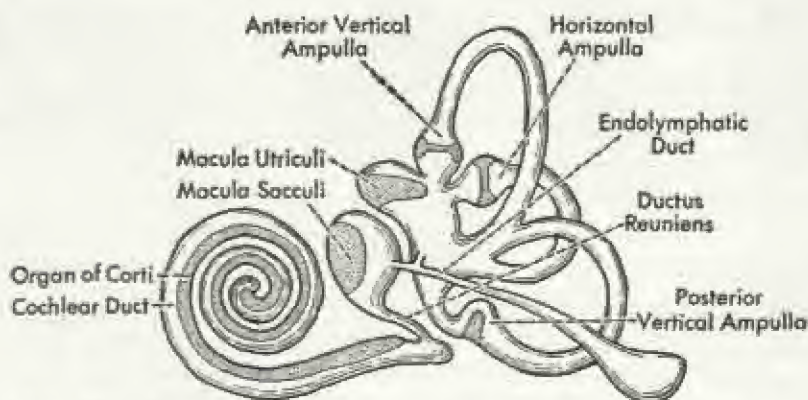


Fig. 696. Diagram of the right membranous labyrinth as seen from medial side. Neuro-epithelial areas are dotted. (After von Ebner and Schaffer.)

ampullaris in the ampulla of each semicircular canal, as already described; the *macula utriculi* in the wall of the utriculus; the *macula sacculi*, in that part of the sacculus that is not drawn out to form the cochlear duct; and the *organ of Corti* in the cochlear duct (Fig. 696). The *cristae* and *maculae* are innervated by the *vestibular branch* of the acoustic (VIIIth) nerve while the *organ of Corti* is supplied by the *cochlear branch* of the same nerve.

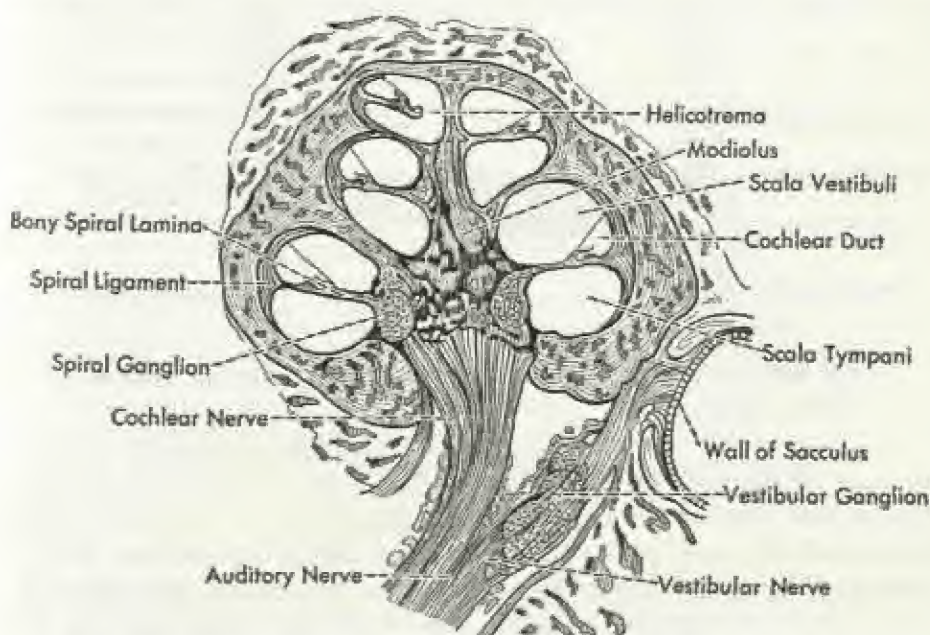


Fig. 697. Axial section through a decalcified cochlea of a new-born child. (After Toldt.)

In the adult human ear, only a slender tube, the *utriculo-saccular duct* connects the utriculus with the sacculus. From this duct a slender *endolymphatic duct* extends to the inner surface of the petrous bone where it enlarges into the *endolymphatic sac* lying just beneath the dura. The sacculus is also connected with the cochlear duct by a slender canal, the *ductus reuniens*.

The bony cochlear canal, in which lies the cochlear duct, spirals about a conical axis, the *modiolus* (Fig. 697). From the modiolus a shelf of bone, the *spiral lamina*, projects into the canal, somewhat like the thread of a screw. Extending along the opposite wall of the canal is the *spiral ligament*, a thickened portion of the periosteum.

In cross sections of the cochlea the cochlear duct appears triangular

(Figs. 697 and 698). One side of the triangle lies against the outer wall of the canal in contact with the spiral ligament. Another side, the *basilar membrane*, extends from the ligament across the canal and onto the upper surface of the spiral lamina. The third side is the thin *vestibular membrane*, or *Reissner's membrane*, which extends from the spiral lamina obliquely across to the upper part of the spiral ligament. Thus in cross section (Fig. 698),

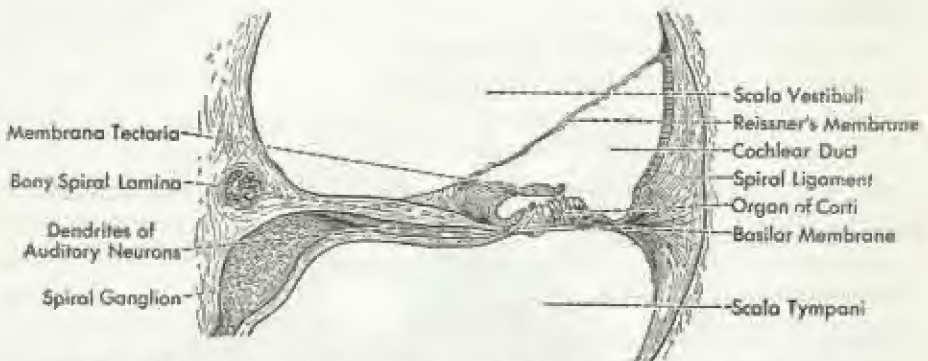


Fig. 698. Axial section through one of the whorls of the cochlea. (After Toldt.)

the bony cochlear canal encloses three cavities. Above the cochlear duct is a perilymphatic space, the *scala vestibuli*, bounded by the vestibular membrane and the upper wall of the bony canal. Below the cochlear duct is another perilymphatic space, the *scala tympani*, bounded by the wall of the bony canal, the bony spiral lamina, part of the spiral ligament, and the basilar membrane. The third cavity is the *scala media*, or cavity of the cochlear duct itself, which is filled with endolymph.

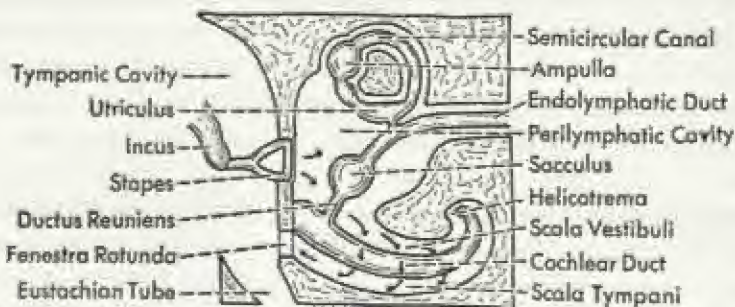


Fig. 699. Diagrammatic section through the internal ear of man, showing by arrows the course of vibrations in the perilymph. (After Burton-Opitz.)

Near the apex of the cochlea the cochlear duct ends a short distance from the end of the bony canal. Consequently the vestibular and tympanic scalae become continuous at this point in a narrow space known as the *helicotrema* (Fig. 697).

The basal end of the cochlear duct lies against the wall separating the air-filled middle ear cavity from the fluid filled cavity of the bony labyrinth (Fig. 699). At the basal end of the scala vestibuli is the fenestra ovalis, also known as the *fenestra vestibuli*. This window is closed by a membrane to which the enlarged "lower" end of the stapes is attached. At the basal end of the scala tympani is the fenestra rotunda also known as the *fenestra tympani* or, more commonly and less appropriately, the *fenestra cochleae*.

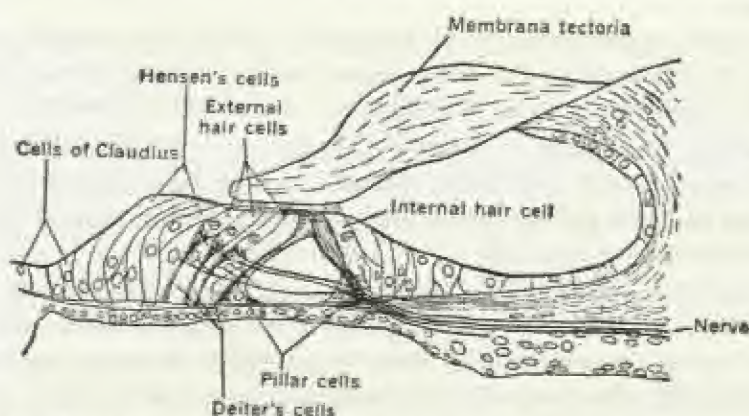


Fig. 700. Cross section through the organ of Corti, within the membranous labyrinth (cochlear duct). (After Szymonowicz.)

Inside the cochlear duct and supported on the basilar membrane are orderly rows of differentiated cells running lengthwise, like a striped ribbon, to the tip of the cochlea (Fig. 700). These rows of cells form the *organ of Corti*, or the receptor apparatus for hearing, named in honor of Alphonso Corti (1822-1876), who in 1851 first discovered many microscopic details of the inner ear.

The most important cells of the organ of Corti in man are the several rows of *hair cells*, which are the phonoreceptors proper. They are connected with neurons of the auditory nerve that transmit to the auditory centers in the temporal lobes of the cerebral cortex the vibratory stimuli received. The hair cells in the human ear are variously estimated to be from 13,000 to 54,000 in number, each one with perhaps 40 cilia, or "hairs" at the receptive end, projecting into the endolymph. They are arranged along the basilar membrane in two bands separated from each other by two rows of

supporting *pillar cells* that lean against each other so as to form an archway.

The inner band of hair cells consists of a single row while the number of rows in the outer band varies, there being three in the basal coil of the cochlea, four in the middle coil and five in the apical part. The rounded base of each hair cell rests upon a supporting cell, *phalangeal* (*Deiter's*) *cell*, which in turn rests upon the basilar membrane. Additional supporting cells make up both the inner and outer edges of the organ of Corti, those of the inner edge being known as *border cells*, those of the outer edge as the *cells of Hensen*. The latter grade over into the *cells of Claudius* which lie along the outer part of the basilar membrane and extend onto the spiral ligament.

From the upper surface of the bony spiral lamina there extends into the endolymph a somewhat flat ribbon-like structure, the *membrana tectoria*, the outer free edge of which extends as far as the cells of Hensen. Its exact relationships are difficult to determine because its outer free edge tends to curl up when treated with fixing reagents. It is probable that in the living condition its lower surface lightly impinges upon the free ends of the hair-like processes of the hair cells.

Along the inner wall of the cochlear canal, following the line of attachment of the lamina spiralis to the modiolus, is a group of nerve cell bodies making up the *spiral ganglion*. From this ganglion dendrites run through the lamina into the organ of Corti where their terminal branches are associated with hair cells. The neurites of these neurons run out through the base of the modiolus as the cochlear branch of the acoustic nerve.

(c) **Physiology of Hearing.**—Sound waves, originating at some sonorous outside point in the form of material particles of air hitting upon one another, reach the ear drum and set it into vibration, if the pressure on the two sides is equalized. The vibrations of the drum are handed on to the chain of ear bones that span the tympanic chamber of the middle ear. The last bone in this chain, the stapes, fitting into the fenestra vestibuli, acts as a rocking plunger that agitates the perilymph in the scala vestibuli (Fig. 701).

Pressure changes in the perilymph are transmitted through the thin vestibular membrane to the endolymph within the cochlear duct. These changes cause movements of the basilar membrane which not only lead to stimulation of the cochlear nerve, as described below, but also affect the pressure in the scala tympani. Any tendency to generate excessive pressure in the practically incompressible fluids of the internal ear is offset by the secondary tympanic membrane which bulges outward, into the middle ear cavity, with each inward movement of the stapes. The passage of fluid

through the helicotrema, as an aid in equalizing pressure differences in the two perilymphatic scalae, is now considered to be of negligible significance because of the small diameter of this region, located at the point farthest from the stapes which brings about the initial pressure changes in the fluid.

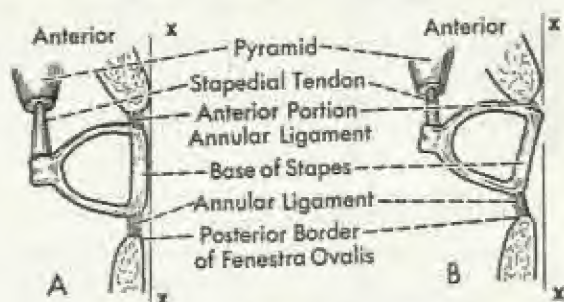


Fig. 701. Schematic representation of the displacement of the stapes, due to the contraction of the stapedius muscle. A, stapes in repose; B, stapes during contraction of the stapedius muscle. The anterior portion of the annular ligament of the stapes is longer than the posterior portion. x-x, antero-posterior diameter of fenestra ovalis, passing through base of resting stapes. [After Testut.]

According to the most generally accepted theory of hearing, a modification of the resonance theory proposed by Helmholtz many years ago, any given frequency causes most vigorous movements of only a localized area of the ribbon-like basilar membrane. There is thus a place on the membrane for each pitch (or frequency); hence, this is known as the *place theory of hearing*. Striking of the hair-cell "hairs" of the affected region against the tectorial membrane stimulates their associated nerve endings. Impulses carried by certain fibers of the cochlear nerve are then interpreted by the cerebral cortex as particular tones. In support of this theory is the work which has shown that the higher audible frequencies stimulate fibers associated with the basal part of the cochlear duct, where the basilar membrane is narrowest, while low frequencies affect the apical region where the membrane is widest (Fig. 702).

The *amplitude* of the vibrations determines the *loudness* of the tones produced, while the *pitch*, whether it be high or low, is correlated with the *frequency*, or relative number of vibrations per unit of time. The quality, or *timbre*, of a tone, by which the difference between a human voice and a violin, for example, is detected when producing the same musical note, is dependent upon the *character*, or shape, of the sound waves when visually recorded, as also upon the *overtones*, or accompanying sympathetic vibrations of different harmonious nodal lengths which may be added to the

fundamental tone. Vibrations without uniformity in wave length or shape fall upon the ear as "noises," while vibrations repeated with regularity of form and shape give rise to "tones."

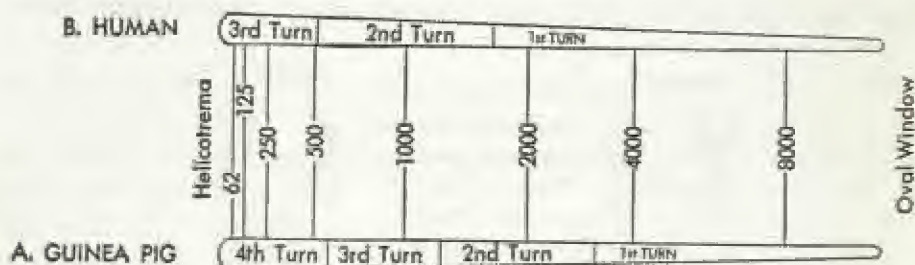


Fig. 702. Scheme of basilar membrane of the cochlea, represented as rolled out flat, to show distribution of pitch reception along the membrane. A, map of basilar membrane of guinea pig, derived from experimental data; B, map of human basilar membrane, deduced from that of the guinea pig. (After Stevens, Davis and Lurie.)

(d) **Comparative Anatomy.**—There is no ear in amphioxus. Among cyclostomes the membranous labyrinth in *Myxine* is a simple undifferentiated sac with one single semicircular canal. In *Petromyzon* two canals are present, with a constriction in the sac that indicates the beginning of a separation into utriculus and sacculus. A *macula communis* in the saccular end, along with a crista in each ampulla, represents the nerve terminals.

In fishes generally the ear hardly rises above the static function of equilibration. Three well-developed semicircular canals and a primitive sacculus, provided with *otoconia* or an *otolith*, offer anatomical evidence that the ear of fishes is static rather than auditory in function. On the posterior side of the sacculus is a small outpocketing, the *lagena*, in which is a sensory area, the *macula lagenae*, of doubtful function (Fig. 703). There are also cristae ampullares, in the semicircular canals, a macula utriculi and a macula sacculi. In addition these animals have another utricular sensory area, the *macula neglecta*, which is double in some cases. It is extremely doubtful whether fishes can "hear," although they respond readily to certain types of jarring or vibration, by means of their lateral-line organs. Whatever vibrations from the surrounding water reach the labyrinth of the ear, do so through the skull or through the spiracular opening, for no middle ear or outer passage-way is yet elaborated. Another reason why fishes are probably oblivious to sounds borne on the air is that, although sound waves transferred under water or through solid objects, as a telegraph wire for example, travel more readily than in air, it is very difficult for vibrations to pass unhindered from thin air into the denser medium of water.

In frogs and toads but not in urodeles, the spiracular cleft enlarges into the tympanic cavity, which is not properly a "middle ear" since no external ear is present. A large external ear drum, connected by a columella with the internal ear, is placed at the level of the skin, and is consequently much exposed to injury. The first true auditory nerve terminals appear in amphibians in the form of the *macula neglecta* and the *papilla basilaris*, the latter structure being of importance since it is the forerunner of the organ of Corti which becomes incorporated within the *lagena* that later coils to form the cochlea duct.

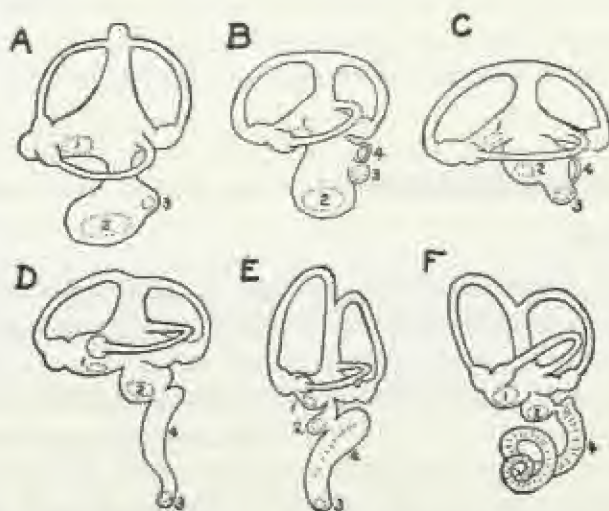


Fig. 703. Lateral-view diagrams of the left labyrinth of the ear. A, teleost; B, frog; C, turtle; D, crocodile; E, bird; F, mammal. 1, macula utriculi; 2, macula sacculi; 3, macula lagenae; 4, basal papilla. (After Hesse.)

The *macula neglecta* continues to be represented in reptiles and birds but disappears in mammals. The ear drum becomes sunken in reptiles and birds, forming a pit which is the beginning of the external auditory canal. Some lizards and crocodiles have an earfold at the margin of the pit which foreshadows the pinna of the mammalian ear. By means of this fold an alligator is enabled to close the short auditory canal while submerged in water. "Horned owls" and certain other birds have the earfold supplemented by upstanding feathers. The tympanic cavity of snakes and legless lizards is much reduced or absent, since direct contact with the ground is the means employed for the reception of seismic vibrations on the part of these highly thigmotactic animals. In birds and crocodiles the two Eustachian canals form a median duct that enters the mid-dorsal region of the pharynx by a

single opening. The lagena elongates and becomes slightly curved in crocodiles and birds.

In mammals the lagena curves still more to form the compact spiral space-saving *cochlea*. The number of turns in the cochlea of various mammals is as follows: *Echidna*, $\frac{1}{2}$; whale, $1\frac{1}{2}$; horse, 2; rabbit, $2\frac{1}{2}$; man, $2\frac{3}{4}$; cat, 3; cow, $3\frac{1}{2}$; pig, 4; South American "paca," *Coelogenys*, 5. The cochlear duct becomes attached along two sides of the bony canal thus dividing the perilymphatic space into the *scalae vestibuli* and *tympani*. The establishment of the *fenestra tympani* as a safety valve against excessive vibrations is a further mammalian refinement. The malleus and incus of the middle ear are also added in mammals, while the auditory canal of the outer ear becomes elongated and bent, thus affording greater protection to the ear drum.

VII. PHOTORECEPTORS

1. In General

The most important and far-reaching of all the sensory avenues of knowledge concerning the external world is through the sense of sight, which pictures not only the changing scene, but also records place, movement, and distance of outside objects. Most of the other senses, such as taste, smell, touch, and temperature, furnish information concerning only the immediate environment. It is true that the radius from which impressions arrive is much enlarged by the sense of hearing, but hearing after all is confined to geographical distances even when augmented by the marvelous mechanical extensions that are made possible by radio. Although one must travel in order to "see" distant lands that lie beyond the horizon, as well as to come into contact with distant stimuli of any sort, it is quite possible to stand still upon a starry night and *see* the heavenly bodies that mark the very outposts of the known universe. What an infinitude of space is comprehended in the statement that *one can see a star!*

None of the human senses is so sorely missed as sight. After Beethoven became deaf and could no longer hear the musical harmonies which teemed in his fertile brain, he became an object of sympathy, but a blind astronomer or painter, living upon memories of what he can no longer see, would surely be a sadder figure.

Nevertheless, sight is by no means an universal or an indispensable endowment of animals, for many creatures are sightless, or "love darkness rather than light."

Eyeless plants are more dependent upon light than animals are, and

although all organisms alike owe their existence either directly or indirectly to the light of the sun and the marvel of photosynthesis, it is not always necessary for so elaborate a receptor as an eye to be involved in reactions to light.

Photoreceptors, which are structures adequate to respond to the stimulus of light, include much more than "eyes." In fact protoplasm generally is more or less sensitive to light, and the function of sight may be regarded simply as a specialized extension of this peculiar type of irritability.

2. Photoreceptors That Are Not Eyes

If the eyeless earthworms did not retire to the safety of their burrows at break of day, after their nocturnal wanderings, the proverbial "early bird" would quickly eliminate them in the struggle for existence. They are able, however, by means of certain specialized *photoreceptive cells* in the skin, to distinguish light from darkness and so usually to escape such a fate.

Many protozoans, as well as larval forms of metazoans in which cellular elaboration of eyes is quite out of the question, nevertheless respond very definitely to the stimulation of light. They are said to be *positively phototropic* when they turn toward the source of light, and *negatively phototropic*, when they turn away. Usually these responses are beneficial to the animal concerned but not invariably so, for positively phototropic moths are known to be killed by flying into a flame.

As highly developed an animal as a vertebrate may possess photoreceptive integumentary cells located outside the eyes, as proved by the behavior of certain chameleon-like lizards, which normally respond to light by color changes in the skin, and which make this response when temporarily blinded, if a stimulating ray of light in an otherwise darkened room is focussed upon the skin.

3. Eyes

Eyes are the photoreceptive organs *par excellence*. They may be described as of two different general sorts, namely, *direction eyes*, that distinguish light and dark and enable an animal to locate the source from which the stimulus comes, and *image-forming eyes*, that report to the brain a more or less definite picture, reflected from objects in the environment.

(a) **Direction Eyes.**—*Direction eyes* are typically shown in non-parasitic flatworms, or Turbellaria, which are found in the daytime out of reach of their enemies clinging to the underside of stones and sticks submerged in shallow water.

The photoreceptive cells in direction eyes are packed closely together

behind shieldlike cups of pigmented cells that are not penetrated by light (Fig. 704). The angles at which these cups are placed on the two sides of the head is such that it permits the light, whenever it does not fall exactly parallel to the long axis of the body, to stimulate the photoreceptors on one side more than on the other side, so that the worm responds by turning until the stimulation received on both sides is equal. This results in *orientation*

with reference to the source of light, and in a negatively phototropic flatworm, tends to carry it into darkness and safety.

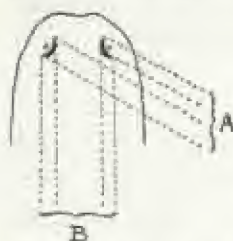


Fig. 704. Direction eyes of a flatworm. A, diagonal direction of light; B, posterior direction of light; x, position of the photoreceptive cells within the crescentic pigment cup, which acts as a shield.

(b) **Image-forming Eyes.**—*Image-forming eyes* are optical devices that not only differentiate between the presence or absence of light, but also receive reflected light in such a way as to transfer a picture to the brain.

There are two outstanding types of image-forming eyes, namely, *mosaic* and *camera* eyes. The former reaches its highest elaboration in the faceted eyes of insects, which far outnumber all other animals having eyes of any kind, but the latter is of greater present interest, because it is the type of the vertebrate eye.

Behind each facet of the compound eye of an insect are several parts which together constitute a separate optical instrument for receiving light that has been reflected from external objects. This unit of the compound arthropod eye is called an *ommatidium*. When clustered together, sometimes several hundred in a single eye, ommatidia produce a map of overlapping details that fit together, like the separate elements in a mosaic pattern, to form a single picture in the brain.

Usually the mosaic eyes of insects are set immovably in the head, but the convex exposure of their surfaces is such that the marginal ommatidia may point outward at angles sufficient to include in the whole eye a wide range of vision.

In crustaceans it is usual for the mosaic eyes to be so mounted upon movable stalks that they may be turned in various directions, without the necessity of moving the rigid neckless head.

4. Human Eyes

A parallel between the typical *camera eye* of a vertebrate and a photographic camera holds good in numerous details. Both are dark chambers which admit the light through a focussing lens and which are guarded by a diaphragm and a shutter-like arrangement that regulate the amount of

entering light. Both have a sensitive receiving surface, lining the side of the chamber opposite the window where the light comes in, and in both there is an inversion upon the sensitive screen of the image received. In one case the picture impressed upon the sensitive plate is "developed" after removal to an appropriate bath of chemicals. In the other instance the picture, received upon the sensitive retina of the eye, is transmitted by the optic nerve to the brain, which becomes its "developer."

The eyeball, or "camera box" of the vertebrate eye, is safely lodged in a bony orbit of the skull, forming a protection to it from mechanical injuries, except for a small though necessary exposure on the front face. It is held loosely in place by a loose system of connective tissue fibers which permits considerable freedom of movement within the orbit.

The walls of the eyeball consist of three concentric layers of diverse tissues. The outer layer, or *tunica fibrosa*, is skeletal in function, maintaining the rigidity of the spherical eyeball (Fig. 705). It is so tough that acids or

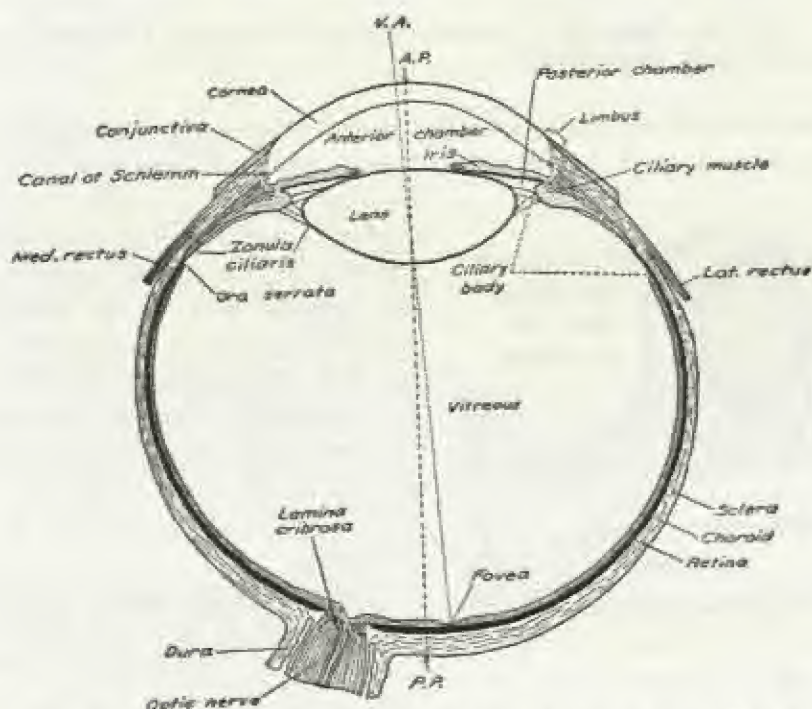


Fig. 705. Horizontal meridional section through the right eye of man, schematic. A. P., anterior pole; P. P., posterior pole; V. A., visual axis. (From Smith and Copenhagen, *Bailey's Text-Book of Histology*, copyright 1944, by permission of Williams and Wilkins, publishers. After Salzmann.)

alkalis, or even cooking, does not destroy it, and it is quite possible to pick a splinter off its exposed surface without serious injury.

The middle pigmented layer, or *tunica vasculosa*, provides a place for nutritive blood vessels, while the inside double *retinal layer* is sensory, containing among other elements the *rods* and *cones* that constitute the essential photoreceptive cells, to which all the other parts of the complicated visual apparatus are subsidiary.

(a) **Development.**—The nervous elements of the eyeball arise from the wall of the embryonic brain. Early in development, before the medullary



Fig. 706. Outgrowth of the optic vesicles and formation of the lens in the chick. (After Duval.)

groove is closed into a tube, the diencephalon gives rise to two outpocketings (Fig. 706). Each of these soon differentiates into an enlarged distal portion,

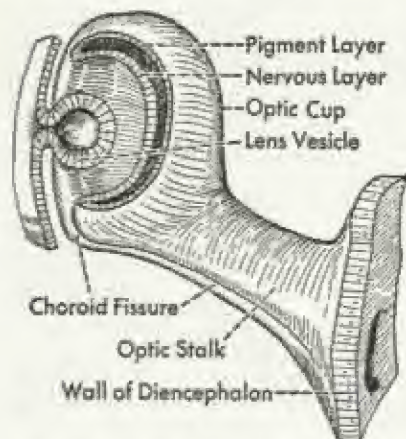


Fig. 707. The optic cup and lens in stereograms, showing choroid fissure. (After Arcy.)

the *optic vesicle*, and a constricted proximal *optic stalk* which connects the vesicle with the diencephalic region. Next the terminal part of the vesicle invaginates to form a two-layered *optic cup* with its concavity toward the surface of the body. The inner layer of the cup eventually becomes the *nervous portion of the retina*, while the cup's outer layer forms the *pigment layer of the retina*.

As the primitive double cup is forming, a portion of its ventral brim is involved in the invagination so that a deep notch, the *choroid fissure*, develops in this region (Fig. 707). This infolding also continues along the optic

stalk to form a ventral groove which extends as far as the diencephalic wall.

Eventually certain of the retinal neurons send out neurites which, after passing through the choroid fissure, run along the groove in the optic stalk and into the brain. These neurites form the optic nerve, while the optic stalk fades in importance and vanishes. Complete closing of the choroid fissure by the growth of surrounding cells about the optic nerve causes the latter to have the appearance of penetrating directly through the wall of the eyeball.

Meanwhile, at the point where the optic cup comes nearest to the surface ectoderm, the latter gives rise to the *lens*. Lens formation is brought about by the invagination of the thickened ectoderm, which eventually pinches off a hollow vesicle that becomes entirely disconnected from the outside ectoderm. The cavity within the embryonic lens is gradually obliterated by the columnal growth of cells which make up its inner part and which eventually fill the space entirely (Fig. 708).



Fig. 708. Development of the lens. (After Kingsley.)

The retina and lens later become enveloped by mesenchymal tissues which give rise to the two outer layers of the eyeball, the *tunica vasculosa* and the *tunica fibrosa*.

(b) **Structure of the Human Eye.**—The outer *tunica fibrosa* of the human eye is made up of the *sclera* and the *cornea* (Fig. 705). The *sclera* is a tough, opaque layer of interwoven fibrous connective tissue. Commonly known as the “white of the eye,” it occupies five-sixths of the entire circumference, but is mostly out of sight within the orbit. It is pierced by the optic nerve and also by blood vessels.

The remaining one-sixth of the fibrous layer forms a transparent circular window, the *cornea*, over the front face of the eyeball and continuous with the white sclera. It is thinner in front (0.9 mm) than around the ring at the corneo-scleral margin (1.2 mm), where the muscles that rotate the eyeball in the socket are attached. The cornea is an important part of the focusing mechanism of the human eye, having a refractive power about two and one-half times that of the lens. Much of the importance of the lens, therefore, is associated with its use in accommodating the eye to objects at various distances from it.

The middle, vascular layer, or *tunica vasculosa*, which is in intimate contact with the layers next to it, both inside and out, is made up of three general parts continuous with one another, namely, the choroid, ciliary body, and iris.

The *choroid*, making up most of the middle layer except its anterior part, is rich in blood vessels and pigment cells. As a result of the heavy pigmentation of this part, light is absorbed instead of being reflected back and forth inside the eye. Toward the front of the eyeball the vascular layer becomes thickened into the *ciliary body* which is attached to the inside of the sclera, near the sclero-corneal junction, in the form of a ring. The portion of the vascular layer encircled by the ciliary ring and behind the cornea is the *iris*, which is not attached to the outer fibrous layer as are the choroid and ciliary body. In the center of the disc-like iris is an opening, the *pupil*, which always appears black in man because it is the only place through which light may enter into the dark camera-box, lined with non-reflecting tissue.

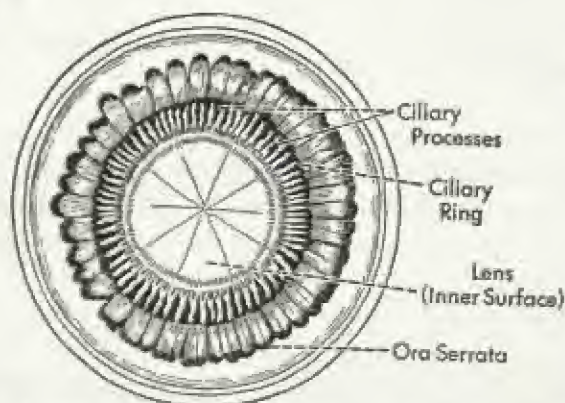


Fig. 709. Anterior half of the eye seen from within. (After Salzmann.)

Beginning with a relatively thin edge next to the choroid, the *ciliary body* gradually increases in thickness until the maximum is reached near the margin of the iris (Fig. 705). The most conspicuous parts of this body are the ciliary processes and the ciliary muscles. The *ciliary processes* are 70 to 80 radiating ridges composed chiefly of connective tissue, blood vessels, and pigment cells (Fig. 709). The sides of these ridges and the valleys between them furnish the points of attachment for the *suspensory ligament* that stretches from them to the capsule surrounding the lens.

The *ciliary muscles* have to do with changing the shape of the lens so as to focus images sharply upon the retina. These muscles, smooth and involuntary, are innervated by fibers of the oculomotor nerve. Their action, however, is much more rapid than that of most smooth muscles. They include both circular and radial fibers, with the origin ends of the latter attached to the sclera near the junction of the sclera with the cornea. Thus

contraction of the ciliary muscle fibers pulls the choroid forward and reduces the diameter of the ciliary body.

The *iris* serves as a delicate diaphragm surrounding the pupil. Within it are two antagonistic muscles, the *sphincter pupillae* and the *dilatator pupillae*, the contractions of which serve respectively to decrease and to increase the size of the pupil. In this manner the iris regulates the amount of light admitted into the eye. By covering the outer more curved edge of the lens it also cuts down or prevents the occurrence of spherical or chromatic aberration, which would blur or confuse the images cast upon the retina. When a person "goes to the light" to examine an object carefully, it is usually not because of a scarcity of light available, but because increased light by narrowing the pupil cuts out side lights and thus sharpens the vision, just as closing the diaphragm in a camera reduces spherical aberration and sharpens the image.

Pigment of various kinds, abundant in the iris, gives the characteristic "color of the eyes." A thick *pigment epithelium* forms the posterior surface of this structure in all individuals. In the absence of other pigment, light reflected from this layer appears blue. Whenever any other eye color, such as gray or brown, is shown, it is due to the deposition of additional pigment in the outer parts of the iris where they conceal the blue derived from the pigment epithelium. The eyes of albinos appear pink because, in the complete absence of all iris pigments, the color of the blood shows through this region.

The two muscles of the iris, its pigment epithelium, and the innermost layers of the ciliary body do not properly belong to the tunica vasculosa, but are ectodermal derivatives of the embryonic optic cup. In the iris, the outer layer of the cup gives rise to the muscles, while the inner layer of the cup becomes the pigment epithelium.

The *retina*, the inner or sensory layer of the eyeball, is derived from the two layers of the optic cup and is therefore really a part of the brain. As mentioned earlier, the outer layer of the cup gives rise to the non-nervous pigment epithelium of the retina, which rests against the choroid. The inner layer of the cup forms the nervous portion of the retina, composed of three sets of neurons in series with one another, namely: photoreceptors, inter-

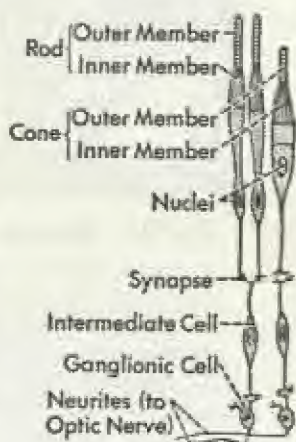


Fig. 710. Diagram showing the three principal layers of the retina, with two rods and one cone in the outer layer, made up of receptor neurons. (After Watson.)

mediate neurons, and ganglionic neurons (Fig. 710). The retina terminates abruptly near the periphery of the ciliary ring, although derivatives of the optic cup continue along the inner portion of the ciliary body and iris. The irregular anterior margin of the retina is known as the *ora serrata* (Fig. 709).

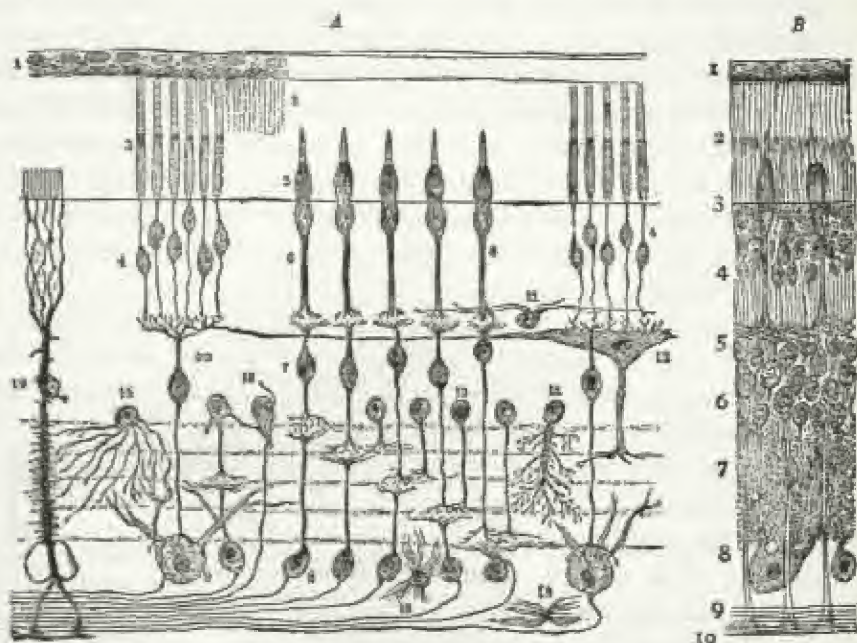


Fig. 711. Diagram showing detail of structure of the retina.

A. 1, pigment epithelium; 2, processes of pigment epithelium cells; 3, rods; 4, rod nuclei and fibers; 5, cones; 6, cone fibers; 7, cone bipolar cells of inner nuclear layer; 8, smaller cells of ganglion layer; 9, larger ganglion cells; 10, ganglion cell axons forming nerve fiber layer; 11 and 12, horizontal cells; 13, 14, 15, and 16, amacrine cells; 18, neuroglia cells; 19, Müller's fiber; 20, rod bipolar cell of inner nuclear layer.

B. 1, pigment epithelium; 2, layer of rods and cones; 3, external limiting membrane; 4, outer nuclear layer; 5, outer plexiform layer; 6, inner nuclear layer; 7, inner plexiform layer; 8, layer of ganglion cells; 9, nerve fiber layer; 10, internal limiting membrane. (From Smith and Copenhagen, *Bailey's Text-Book of Histology*, copyright 1944, by permission of Williams and Wilkins, publishers.)

The *photoreceptors*, *rods* and *cones*, are next to the retinal pigment cells, from which fine cytoplasmic processes extend down between the outer segments of these receptor cells (Fig. 711). Cones are primarily concerned with color vision, while rods are chiefly useful in colorless vision at low light intensities. According to the most reliable estimates the retina includes

7,000,000 cones and 100,000,000 or more rods, all packed closely together like matches in a box, each one registering a single point of reflection from outside illumination. In the human eye, rods and cones differ more in size than in shape, yet their names are still descriptive of their form.

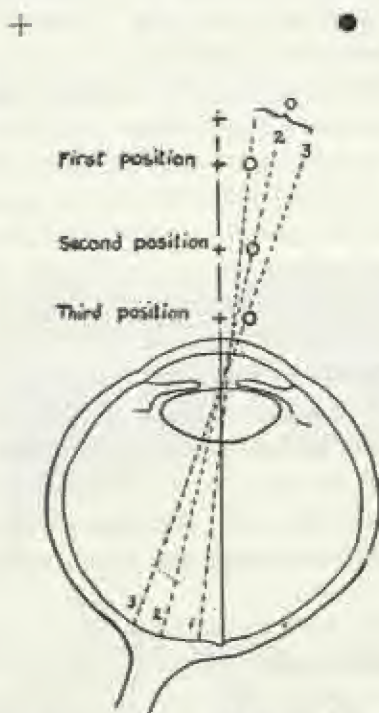


Fig. 712. The blind spot of the eye. Hold the black figure straight in front of the eyes about a foot distant. Close the left eye and look at the white cross. You will see the round white spot also. This corresponds to the first position in the diagram. Now gradually move the page toward your eye. When you reach the second position the round spot will disappear, because the rays of light from it now fall upon the place where the optic nerve enters the eyeball and not upon the rods and cones of the retina. If the page is moved still nearer, the round spot will reappear, because light reflected from it now strikes the retina on the other side of the optic nerve, as shown by position 3.

Vision is dependent upon photosensitive pigments found in the outer segments of rods and cones. The existence of such a substance, called *visual purple* or *rhodopsin*, has been known since 1876. It is abundant in rods and was at one time thought to occur in small quantities in cones. It is now believed that cones have a somewhat different pigment, *visual violet* or

iodopsin. The production of both of these pigments is dependent upon a supply of vitamin A. It has long been known that improper diets may result in night blindness, or loss of sensitivity to dim light. Recently it has been shown that this condition results from the inability to synthesize visual purple in the absence of vitamin A. According to the photochemical theory of Hecht, the photosensitive pigments are decomposed by light with the formation of various products, including at least one which can initiate impulses in the receptor cells of the retina.

Neurites of the rod and cone cells synapse with bipolar *intermediate neurons* which in turn connect with large *ganglionic neurons* (Fig. 710). The neurites of these ganglionic neurons form the optic nerve, after running across the inside of the retina. The point where these fibers converge to leave the eyeball is known as the *optic disc*, or the *blind spot*. Since photoreceptive rods and cones are not present there, rays of light striking it are not seen. The blind spot is like a photographic film with a patch of its surface scratched off. The presence and extent of the blind spot in the reader's eye may be easily demonstrated by reference to Figure 712.

In the stratum of the intermediate cells there are cross-connecting neurons, *horizontal cells* and *amacrine cells*, which join together various retinal neurons. There are also non-nervous *supporting fibers of Müller* extending through nearly the entire thickness of the retina.

It will be observed that the rods and cones, unlike other sensory recep-

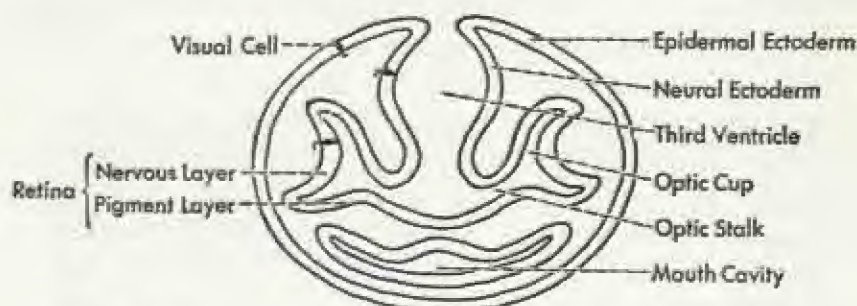


Fig. 713. Diagrammatic transverse section through the head of a hypothetical vertebrate embryo, illustrating Balfour's theory to account for the inversion of the visual cells of the vertebrate retina. In the integument the visual cells face outward toward the source of light. The cavity of the optic cup is seen to be continuous with the outside of the animal, and the surface of the retina next to the cavity of the optic cup is obviously comparable to the outer surface of the integument. Hence the visual cells in the retina face toward the bottom of the cup, and away from the outside of the eye. Thus the retina is inverted, facing away from the source of illumination instead of toward it. (After Parker.)

tors, point *away from* the source of stimulation. Light, upon reaching the retina, first encounters the non-receptive ganglionic and intermediate cells before coming to the receptive rods and cones. This *inversion* of the retina, characteristic of all vertebrates, may be explained, as Balfour suggested, by the embryonic history of the retina. According to Balfour the rods and cones when still in the surface ectoderm faced the outside world from whence the stimulus of light came (Fig. 713). With the invagination of the central nervous system they would therefore face the cavity of the brain. As the cavity between the two layers of the optic cup is really a continuation of the brain cavity, the receptors in the nervous portion of the retina would face this space. Thus the photoreceptors head toward the pigment layer of the retina, or away from the source of light for the completed eye.

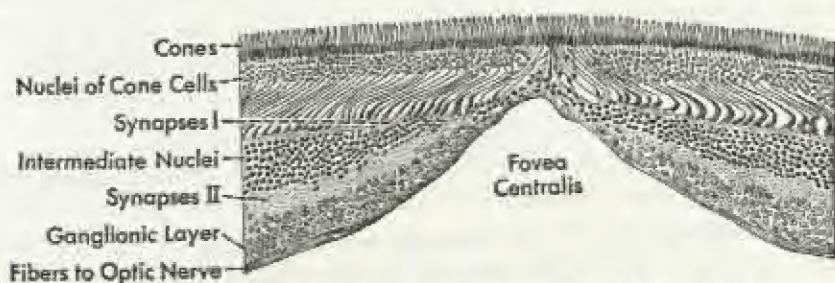


Fig. 714. Section through the human fovea. (After Stöhr)

In the posterior part of the retina in the direct line of the visual axis, is a small yellowish area, the *macula lutea*. In its center is a conical depression, the *fovea centralis*, where the nervous portion of the retina is reduced to a layer of receptor neurons, as a result of the spreading apart of the intermediate and ganglionic layers (Fig. 714). The floor of the fovea, occupied by several thousand long slender cones closely packed together, is the region of greatest visual acuity and color perception, due in part to the great number of photoreceptors, all cones, located here. It is also possible that the spreading of the inner layers of the retina permits a freer passage of light to the photoreceptors. Recently Walls has suggested that the sides of the fovea may act as refracting surfaces which so enlarge the image that more photoreceptors are involved. Thus a clearer image results from the increased resolving power in the foveal area. Whenever we look directly at any object, the image of that object falls on the fovea, while the light from neighboring objects, entering the eye at an angle, falls upon the rods and scattered cones that are distributed in the retinal areas outside the fovea.

Light entering the pupil of the eye at an angle instead of directly in

line with the visual axis falls upon portions of the retina outside of the fovea. It must, therefore, filter through and between the intervening, intermediate and ganglionic cells of the retina before it reaches the receptive rods and cones whose receptive ends extend between the pigmented cells of the outer retinal layer. The amount of light reaching the rods and cones under all these difficulties is regulated, as occasion demands, by the iris, with its adjustable pupillary aperture.

The *lens* is a cellular biconvex structure in which the component parts become transparent. In conjunction with the cornea it serves to refract the rays of light which enter the eye. Thus these rays are concentrated or focused upon the retina, producing a sharply defined replica of the external scene, much smaller in size than that which is presented to the eye. The anterior face, which is somewhat less convex than the posterior, is in contact with the pupillary margin of the iris. Surrounding the lens is a highly elastic capsule to which the *zonular fibers* (*fibers of Zinn*), which make up the suspensory ligaments, are attached near the equator of the lens. Thus these fibers extend from the ciliary body to the lens capsule.

In the resting eye, the short zonular fibers exert a tension, which somewhat flattens the lens, especially its anterior surface. In this state, images of distant objects are sharply focused on the retina. When the ciliary muscles contract, they reduce the diameter of the ciliary body thereby decreasing the tension on the zonular fibers. The elastic lens capsule is thereby allowed to modify the shape of the plastic lens so that it is more spherical, a change that is most pronounced in the anterior part of the lens (Fig. 715). By these delicately controlled changes in the shape of the lens, images of near objects are brought into sharp focus on the retina.

There are three chambers, or cavities, in the eyeball (Fig. 705). The large space behind the lens, and nearly surrounded by the retina, is the *vitreous chamber*, containing the *vitreous body*, a transparent, jelly-like mass. Extending through this body, from the concavity into which the lens fits to the vicinity of the "blind spot," is the *hyaloid canal*, through which an artery runs during embryonic development. Between the cornea and the lens are two spaces which communicate with one another through the pupil. In front of the iris is the *anterior chamber*, behind it the *posterior chamber*, both of which are filled with a watery lymph, the *aqueous humor*.

Communicating lymph spaces are also present in the eyeball. Around the outer margin of the anterior chamber is a loose spongy tissue containing many *spaces of Fontana* which communicate with the chamber. Nearby, at the corneo-scleral junction, in a circular channel, the *canal of Schlemm*, which communicates with neighboring scleral veins by a score or more of

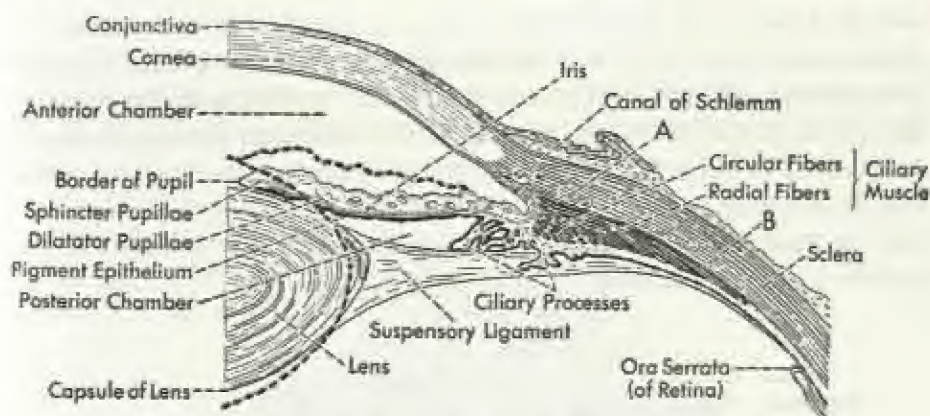


Fig. 715. Diagram illustrating the process of accommodation in the human eye. For near vision the ciliary muscles contract, drawing the region *A* nearer to the region *A*. The tension upon the ciliary ligament being diminished thereby, the lens assumes a more spherical shape, chiefly in the direction of the cornea with a consequent displacement anteriorly of the iris. These changes are indicated by broken lines; in the case of the iris, however, only the anterior surface is shown in the displaced position. (After Toldt.)

small branches (Fig. 715). Although there are no openings from the spaces of Fontana into this canal, it is believed that fluid from the anterior chamber entering the spaces of Fontana may pass into the canal and thence into the blood stream. Possibly excess fluid is removed from the eyeball along this pathway.

(*c*) **Accessory Parts.**—In addition to the eyeball itself there are certain accessory structures, namely, extrinsic muscles, glands, and shutter-like eyelids and eyelashes, that are parts of the complex vertebrate eye region. The *extrinsic muscles*, that enable the eyeball to face in various directions without moving the entire head, have already been considered (Fig. 584). They are inserted on the outside of the eyeball far enough forward so that, when contracted, they do

not pull directly against their point of attachment, but against the curving surface of the eyeball, thus minimizing the liability of tearing loose (Fig. 716).

Eyelids are transverse protective folds of the skin that close like shutters



Fig. 716. Diagram to show that the eyeball muscles are attached so far forward that they pull against the side of the eyeball, as indicated by the arrow, instead of directly at their point of insertion.

over the front face of the eye. The inner surface of the lids, the *conjunctiva palpebrarum* (Fig. 717), is a reddish mucous tissue continuous with the *conjunctiva bulbi* that extends over the eyeball, making a thin transparent skin on the face of the cornea through which light must pass on its way to the retina. The upper lid in man is larger and more movable than the lower, and the aperture between the lids, or the *palpebral fissure*, is rather wider than in most mammals, showing some of the white sclera as well as the circular transparent cornea.

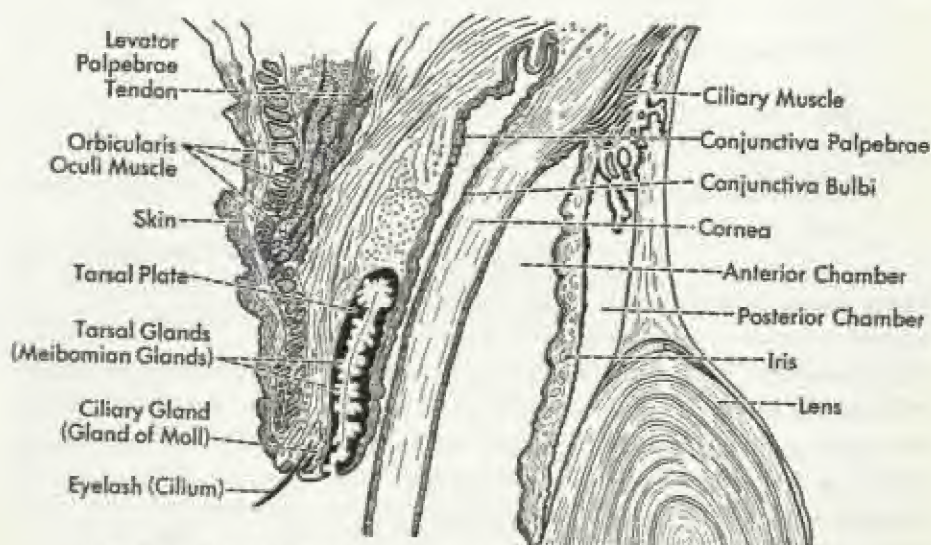


Fig. 717. Vertical section through the upper eyelid and outer part of the eyeball. Note that *conjunctiva palpebrae* (as used in this figure) means *c.* of the eyelid, while *c. palpebrarum* (as used in the text) means *c.* of the eyelids. (After Toldt.)

The edges of the palpebral fissure are supplied with a double row of *eyelashes*, larger above than below, which guard the sensitive conjunctival surfaces against dust particles and similar unwelcome intrusions.

In the inner angle of the eye there is present a vertical fold of the conjunctiva bulbi, called the *plica semilunaris*, that in many vertebrates becomes extended into a movable third eyelid, or *nictitating membrane*, lying under the other two and closing over the eyeball from the inner angle outward (Fig. 718).

At the medial end of each eyelid is a small opening, or *punctum lacrimale*, which leads into a slender canal, or *lacrimal duct*. The ducts from the two eyelids lead into a *nasolacrimal canal*, through which the excess of

tears produced by the lacrimal gland is ordinarily drained into the nasal cavity. Medial to the plica and between the two lacrimal ducts is a small reddish elevation of the conjunctiva, the *caruncula lacrimalis*, which probably has to do with regulating the escape of tears through the nasolacrimal canal.

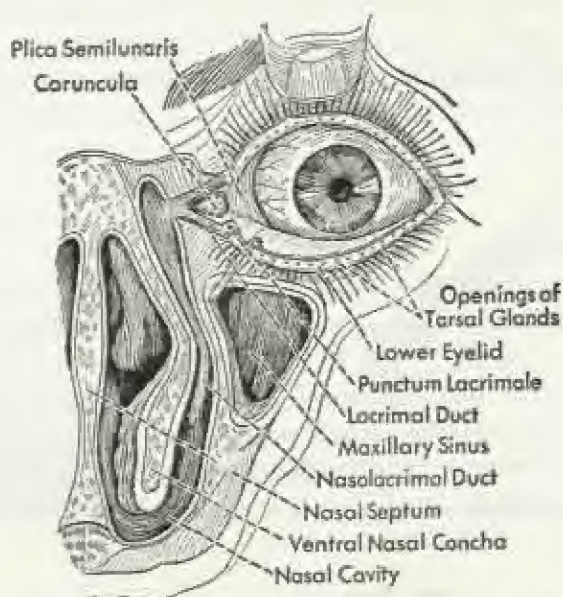


Fig. 718. Front view of left eye showing plica semilunaris, caruncula lacrimalis, and lacrimal apparatus. (After Gray.)

Between the outer skin and the inner conjunctiva palpebrae each eyelid is reinforced by a stiffening fibromuscular layer, the *tarsal plate*, containing numerous *Meibomian glands*, that pour out an oily secretion at the inner edge of the eyelid (Fig. 717). The oily film produced by these glands serves constantly to seal the inner margin of the moving lids to the surface of the eyeball and, when the eye is completely closed, to hold the margins of the two lids temporarily together.

The *lacrimal glands* open inside of the upper lids by several short ducts at the outer angle of the eye. The occasional occurrence in man of lacrimal glands opening inside of the lower lids (Fig. 159) is a reminder of the evolutionary journey they have made in order to arrive at their present position. In amphibians and reptiles these glands open inside of the lower lids.

Tears are a watery secretion from the lacrimal glands and are continually produced, flowing in the form of a thin film over the exposed surface

of the eyeball, to drain eventually through the puncta lacrimalia into the nasolacrimal canal, at the inner angle of the eye. They serve not only to keep the conjunctival and nasal membranes moist, but also to clean the surface of the eyeball of foreign particles that may accidentally find lodgment there.

Weeping, which is accompanied by an overflow of tears, is peculiar to mankind. It is apparently a phyletically recent acquisition connected with certain emotional states that are not present in lower animals. Consequently, as a comparative anatomist would expect, a human baby cannot *weep*, in spite of the presence of lacrimal glands, until it is about six weeks old, although it may repeatedly demonstrate its ability to "cry."

5. Median Eyes

An ancestral median eye, either the parietal or the pineal body arising from the dorsal diencephalic region of the brain, is laid down embryonically in nearly all vertebrates.

In lamprey eels both structures, parietal and pineal, are represented as a pair of organs with the parietal organ on the left and the pineal on the right side respectively, or more commonly with the parietal organ crowded around into a position anterior to that of the pineal body or beneath the latter (Fig. 719).

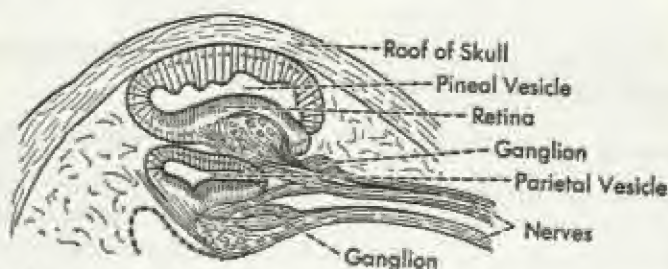


Fig. 719. Median longitudinal section through median eyes of *Petro-myzon*. (After Owsjannikow.)

The *parietal organ* degenerates in the cyclostomes, most fishes, and amphibians, but develops into a structure resembling a true optical organ with a retina and considerable structural complexity in certain lizards, particularly *Sphenodon*.

The extinct stegocephals had a conspicuous foramen through the top of the skull, like that in the skull of *Sphenodon* and certain anurans and lizards, which was probably for the accommodation of some sort of a median eye.

Only a trace of the parietal organ remains in birds, while among adult mammals it entirely disappears, in many cases in the embryo as well as in the adult.

6. Comparative Anatomy

(a) **Amphioxus.**—Eyes are absent in amphioxus, but numerous photoreceptive cells occur in the nerve cord, thus rendering these primitive chordates sensitive to light as it penetrates through the semi-transparent tissues of the body. Each of these cells has a pigment cup associated with it (Fig. 720).

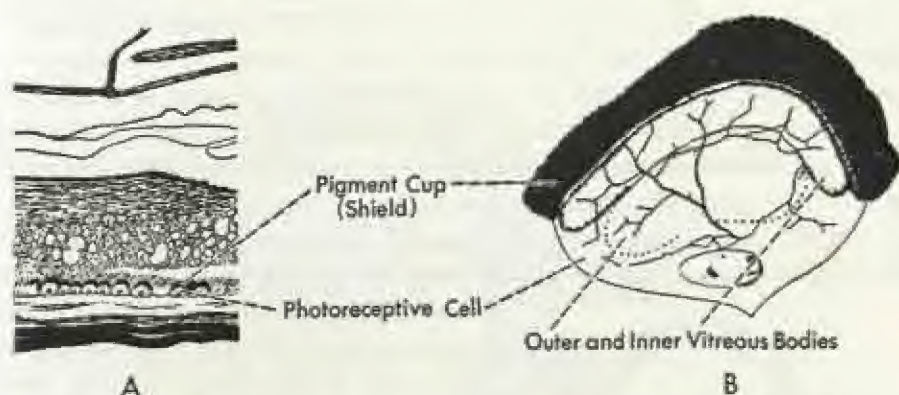


Fig. 720. Photoreceptors of amphioxus. A, sagittal section through ventral part of spinal cord showing light receptor cells in situ; B, a light cell and its shield (pigment cup), showing nerve endings surrounding the so-called vitreous bodies of the cell. (From Kappers, Huber and Crosby, *The Comparative Anatomy of the Nervous System of Vertebrates, including Man*, copyright 1936, by permission of The Macmillan Company, publishers.)

(b) **Cyclostomes.**—The eyes of cyclostomes are degenerate rather than primitive. The eyeball is for the most part small and buried under a thick skin. It lacks cornea, iris, lens, lids, and ciliary apparatus, although *Geotria macrophthalmus*, a fresh-water cyclostome from South America, having unusually large eyes as its name indicates, is an exception. There is no differentiation into rods and cones in the retina, for only elongated rods are present, indicating that rods, which are adapted for the reception of lights, shadows, and the movements of external objects rather than for the reception of colors, are phylogenetically older than cones.

(c) **Fishes.**—The *elasmobranch* eye is provided with a large rounded cornea, that aids the spherical lens in focusing. Partial compensation for the difficulty in seeing both forward and backward with an eye placed on the

side of a rigid neckless head, is furnished by the lens that projects *through* the pupil against the cornea, so that "rays" of light coming at an extra wide angle are caught and concentrated upon the retina.

Eyelids, which are plainly simple folds of the skin, are present in many elasmobranchs but not in other fishes. The outer sclerotic layer is frequently reinforced by cartilage. The eyelids of the hammer-head shark, *Sphyrna*, are circular, which is perhaps the primitive form of all eyelids. It is easy to see how closure of the eyelids would be greatly facilitated by modification into upper and lower lids.

A *tapetum lucidum*, a layer composed of pigment and light-reflecting crystals, is found in the center of the choroid layer in some cartilaginous fishes. In the outer part of the choroid some teleosts have a silvery or greenish-golden layer called the *argentea*, that likewise acts as a reflector.

The eyes of teleosts vary greatly in size, being large in pelagic carnivorous fishes and certain deep-sea forms dwelling in regions of dim light, but small in bottom feeders. The eyeball is usually much flattened on the front face, so that the optical axis is shorter than the diameter through the equator. No eyelids or glandular devices to keep the eyeball moist are present or

needed, but the unblinking eyes are in some measure shielded from the impact of water during locomotion by their lateral position.

Periophthalmus, the ambitious tropical climbing fish that crawls out of the water and lies in wait for flying insects upon the aerial roots of mangrove trees, has so far improved on the traditional fish eye as to anticipate the winking disappearing eye of the frog, which can be depressed into a protective orbit in the skull, or popped out at will to view the surroundings.

Certain deep-sea fishes possess so-called *telescopic eyes*, with elongated eyeballs, enormous spherical lenses, and rounded corneas directed upward and pointing towards the source of the dim light above them (Fig. 721).

Focusing is accomplished as in a camera by *shifting the position of the lens* with reference to the sensitive retina, while in higher forms the same result is brought about by *changing the shape*, but not the position, of the elastic lens. The eyes of fishes are normally nearsighted, that is, they are

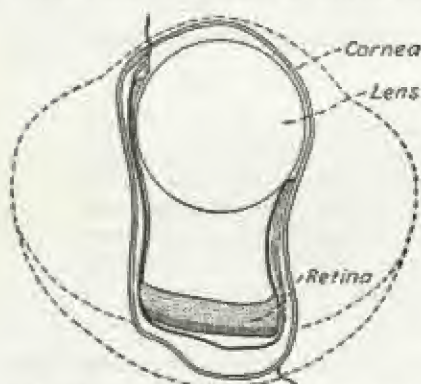


Fig. 721. Median section through the telescopic eye of a deep-sea fish, *Agropelecus*, compared with the dotted outline of the usual eye of a fish. (After Franz.)

accommodated to near objects when at rest, so that focusing by shifting the position of the lens is called for only when more distant objects are to be brought into clear vision. In either case it is not easy to see at a distance through the denser light-absorbing medium of water. The ciliary processes and muscles are small.

The movement of the lens within the eyeball of a teleost fish, but not of an elasmobranch, is probably aided by the *processus falciformis*, a sickle-shaped organ containing blood vessels, nerves, and muscles, and having an enlarged end, the *campanula Halleri* (Fig. 722). It extends from the choroid through the retina to the back of the lens. There is apparently no focusing device in the eyes of elasmobranchs.

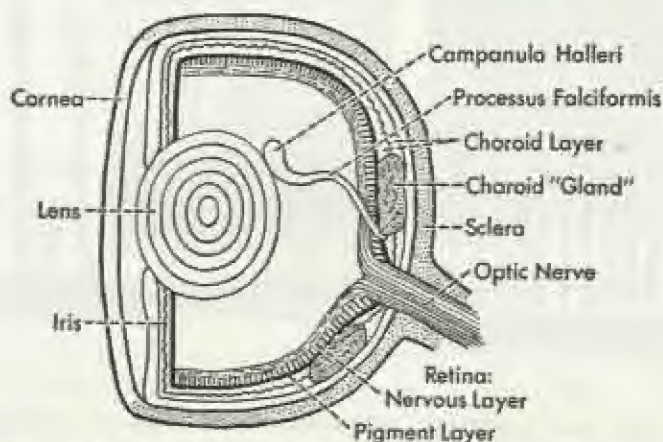


Fig. 722. Diagrammatic vertical section through the eye of a teleost, *Salmo*. (After Parker and Haswell.)

Most fishes are practically color-blind, for a histological examination of the retina reveals a great scarcity, or an entire absence, of color-receiving cones. Some marine teleosts have a fovea.

In fishes there are marked changes in the retina when an animal is transferred from darkness into light, or the reverse happens (Fig. 723). In a dark-adapted animal the retinal pigment has receded from around the rod and cone endings and collected in the bases of the pigment cells. The cones have elongated somewhat, while the rods have shortened, with the result that these two types of cells are of approximately equal lengths. When such an animal is exposed to light the pigment migrates away from the bases of the pigment cells, the cones contract, and the rods elongate into the pigmented area. Many believe that by these changes the highly sensitive outer segments of the rods are made more accessible in dim light or darkness, yet

protected from excessive exposure in strong light. In this manner the retinal changes supplement the activity of the iris in regulating the amount of light which reaches the photoreceptors. This theory does not explain the behavior of the cones and is open to other objections, yet various other theories which have been proposed are equally inadequate. Further data are needed before we can hope to understand the complex activities of the retinal elements.

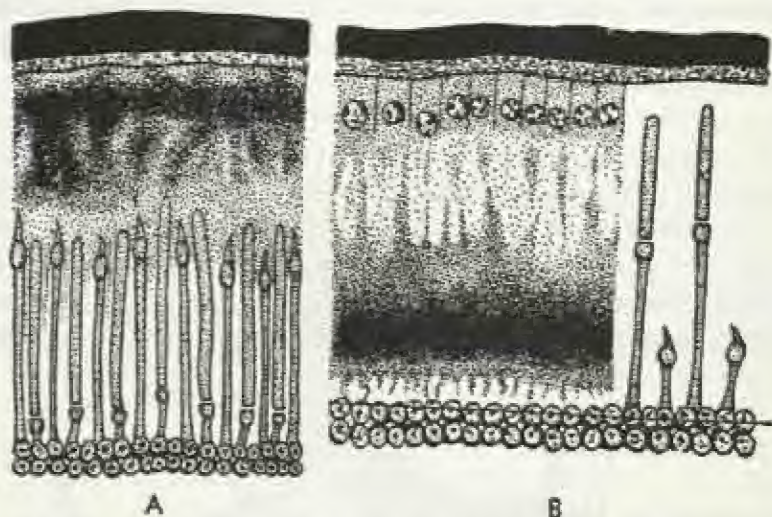


Fig. 723. A, dark-adapted, and B, light-adapted retinas of *Ameiurus*. In A the pigment has receded toward the choroid, the inner member of the cone has elongated, and the inner member of the rod shortened. In B, these processes have been reversed. (From Detwiler, *Vertebrate Photoreceptors*, copyright 1944, by permission of The Macmillan Company, publishers. After Arey.)

(d) **Amphibians.**—In aquatic urodeles generally, the eyes are small, without lids, and often sunken into the skin. These animals apparently see with considerable difficulty, and then only nearby objects that are in motion. Even the anurans, those amphibian aristocrats which are adapted to life on land, possess eyes in many particulars simpler than those of fishes, for, although eyelids and eye glands are present, there is no tapetum or argentea associated with the choroid, and the retina possesses no fovea.

The small lens in the amphibian eye is no longer spherical but ovoid. It is located entirely behind the iris, giving space for the anterior chamber of the eye, while the cornea is so rounded out as to have the focusing value of a second lens, making the animal shortsighted in air when at rest, but

farsighted when submerged under water, since the cornea and fluid in the anterior chamber have practically the same refractive index as that of the water outside, with the result that the cornea fails to focus the light as it passes through. As in fishes, the position rather than the shape of the somewhat inelastic lens is changed in the process of focusing, the ciliary muscles and processes being rudimentary.

The *nictitating membrane* in a frog's eye, unlike that of higher vertebrates, is derived secondarily from the large lower eyelid and is lubricated by the *Harderian glands*, which open into the conjunctival sac beneath it along the lower eyelid. Phylogenetically these are the earliest form of lacrimal glands.

The *iris* of the eye in many amphibians is brilliantly colored, being frequently golden, or shot with yellow flecks.

"Which like the toad, ugly and venomous
Wears yet a precious jewel in his head."

The *pupil* shows much variation in shape, ordinarily being round, but transversely oval in *Rana* and *Bufo*, vertically elliptical in *Alytes*, and somewhat triangular in *Bombinator*.

The rods in the retina are considerably more numerous than the cones. Migration of retinal pigment is extensive in these animals but the rods and cones do not change in length to the same extent as in fishes. In urodeles the length of the rods is not altered by changes in illumination.

(e) **Reptiles.**—The eyes of reptiles are always decidedly lateral in position, so that they have little if any common field of vision. A lizard, for example, may spookily roll one eye upward and the other backward or forward at the same time, thus seeing independently in two different directions at once. With the necessity for adaptation to life on land, the reptilian eye is safeguarded against increasing dangers by means of glands and well-developed eyelids. In addition to the small upper and the larger and more movable lower lids, there is a transparent nictitating membrane inside of the paired eyelids next to the eyeball. Harderian glands supply this third eyelid along the ventral border, while true lacrimal glands for the first time appear in the region of the outer angle of the palpebral fissure. Both Harderian and lacrimal glands find an outlet for the excess of their secretions in the nasolacrimal canal. That the differentiation of tear glands is a comparatively recent acquisition among reptiles is indicated by the fact that *Sphenodon*, which represents the most ancient of surviving reptilian types, is without tear glands.

Snakes, geckos, and certain limbless lizards, living in intimate contact

with the ground, lack movable eyelids. Their staring unwinking eyes are protected by fixed transparent goggle-like windows of skin, shed in ecdysis. Such a transparent window in the closed lower eyelid allows light to enter and is at the same time a protection against blowing sand.

Considerable advance over the amphibian retina is shown in the relative number of cones as compared with rods. In fact diurnal lizards have no rods, while some diurnal turtles have very few. Crocodiles, which have a retina rich in rods, are well adapted for nocturnal vision. The diurnal lizards have better developed foveas than are found in any mammals including man. The iris of the reptilian eye is frequently highly colored, and in some turtles may even be of a different color in the male and female of the same species. The pupil is usually round, but it may be slitlike, either vertically or horizontally.

The reptilian lens is less convex than that of amphibians. Further, for the first time in vertebrate evolution, the lens is elastic so that focusing is effected by the improved method of changing the shape of the lens, rather than by shifting its position as in aquatic vertebrates. The ciliary processes are well developed and the large ciliary muscles are composed of striated fibers, a condition found in no other vertebrates except birds.

(f) **Birds.**—In every vertebrate class *except birds* there are certain species that are either blind or possess only rudimentary eyes, but the sense of sight is absolutely indispensable to these highly modified aviators in the struggle for existence. Although glands and muscles of the eyeball are better developed in mammals, both in complicated structure and efficient working, no other vertebrate eye excels that of birds, particularly birds of prey. The accommodation apparatus in the bird's eye is especially rapid and effective. Chickens, with their eyes focused closely on the work of picking up small grains of food from the ground, become instantly aware of a predatory hawk, sailing like a vanishing speck high overhead. The same hawk can drop with fatal precision upon a tiny field mouse from a height that seems incredible to the possessor of human eyes.

The eye of birds is relatively very large, each eye occupying fully as much space in the skull as the entire brain in some cases (e.g., the owl). If proportionately as large as that of a bird, the eye of an average-sized man would weigh, according to Tiedeman, as much as five pounds.

The eyeball of most birds is not spherical, since it is constricted in the ciliary zone by a sclerotic ring in such a way that the corneal region becomes projecting and very conical and the posterior part larger and more flattened (Fig. 724).

In most birds there is a preponderance of retinal cones. The eye of some

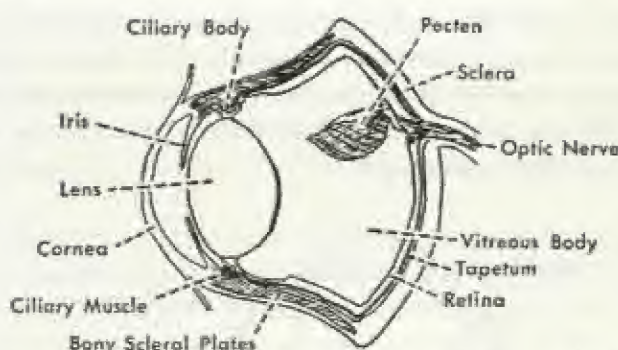


Fig. 724. Schematic section through the eyeball of a bird, *Strix*. (After Haller.)

birds possess two foveal depressions (Fig. 725), although the majority of these animals have only one.

The ciliary processes are large and numerous, frequently numbering more than 100. As in reptiles the ciliary muscles are striated. Both of these features are probably associated with the excellent power of accommodation which birds possess.

Projecting into the vitreous body of the eye is an erectile fanlike organ of several folds, the *pecten*, that bears a superficial resemblance to the processus falciformis of the teleost eye, but is not homologous with it. The pecten arises from the point of exit of the optic nerve while the falciform process is a choroid outgrowth. The initial stages of the pecten appear among certain reptiles (Fig. 726), while embryonic traces of it still persist in the mammalian eye. Its function is not known with certainty but it seems probable that it plays a nutritive rôle and may also regulate the pressure of the fluids within the eye.

Since the iris of the bird's eye contains striated muscle fibers, it is capable of more intensive contraction than is possible in the case of any other vertebrate eye, the iris of which is fitted only with smooth muscles. The color of

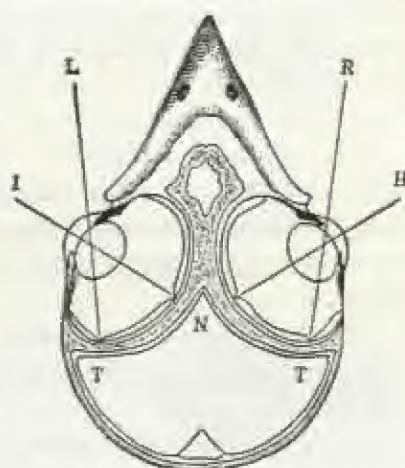


Fig. 725. Section through the head of a swallow, *Tachycineta*, showing the two foveae of each eye. *st*, *sn*, visual axes of the foveae nasales; *tl*, *tr*, visual axes of the foveae temporales. (From Detwiler, *Vertebrate Photoreceptors*, copyright 1944, by permission of The Macmillan Company, publishers. After Wood.)

the iris varies considerably both with age and sex, and is characteristic for different species. In many parrots, for example, it is white, while in cormorants it is green, in swifts blue, and in *Vireo olivaceus* red. The whole expression of the otherwise immobile face of the bird is centered in the lively iris, with its invariably round pupil.

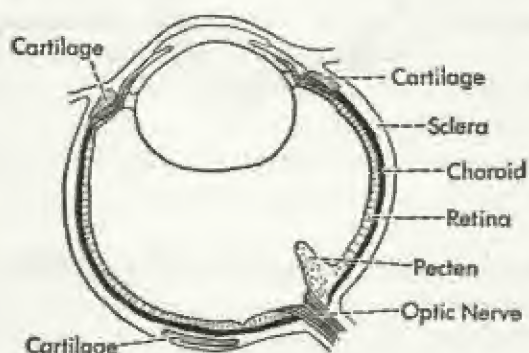


Fig. 726. Diagrammatic horizontal section through the eye of *Chameleon*, showing rudiment of pecten, and sclerotic cartilages. (After Haller.)

The nictitating membrane is well developed and is particularly useful to flying birds, being shut like transparent goggles over the face of the eyeball, thus preventing a flow of blurring tears during flight, which normally would be incited by the stimulating contact of air against the rapidly moving cornea.

Harderian glands are usually large in the bird's eye, while the smaller lacrimal glands occupy the same position as in reptiles, at the outer angle of the palpebral fissure.

Owls have binocular vision, that is, both eyes are trained upon the same field simultaneously. In all birds the act of directing the eyes towards the source of optical stimulation is greatly facilitated by the fact that the extremely mobile head is mounted upon a particularly flexible neck.

(g) **Mammals.**—The mammalian eyeball is nearly spherical. The upper eyelids, unlike those of other vertebrates, are larger and more movable than the lower eyelids, while two rows of eyelashes, lubricated by ciliary glands, are added to the equipment. The nictitating membrane is poorly developed. The eyelids of many mammals, such as mice, rabbits, and cats, are sealed at birth, opening only after several days.

For the most part the tear glands move around to an externodorsal position, although Harderian glands along the ventral margin of the eyelids are

present in whales and such semiaquatic forms as the otter, hippopotamus, and seal.

There is no bony sclerotic ring, but a stiffening cartilage is present in the sclerotic wall of the monotreme, *Echidna*. The sclera of whales is greatly thickened and resistant, possibly to withstand pressure from the surrounding water.

The choroid of the mammalian eye is very rich in blood vessels, whose turgor may in a measure compensate for the lack of skeletal stiffening in the walls of the eyeball. In many mammals, particularly ungulates, cetaceans, and carnivores, there is a light-reflecting *tapetum lucidum* within the choroid layer, but in higher vertebrates including man it is lacking. The eyes of a cat show this reflecting device particularly well at night when lights from an automobile flash into them so that the eyes seem to glow like balls of fire.

The color of the iris varies among mammals generally as it does in man. Thus, there are blue-eyed goats, yellow-eyed cats, and brown-eyed dogs. The pigment determining human eye-color does not reach its final shade until five or six years of age. Aristotle, whose mind was occupied with many things, took time to look into babies' eyes and to note that they are always blue at first. Smooth muscles are present in the iris, as well as in the ciliary apparatus.

In certain ungulates, such as goats, gazelles, camels, and coneys, the edge of the iris shows a peculiar modification, the *umbraculum* (Fig. 727), consisting of pigmented, projecting, granular fringes which permit a lessened amount of light to enter through its ragged edges even when the pupil is wide open. Many heavy-headed ungulates have a pupil in form of a transversely oval aperture that enables the animal to sweep the horizon without swinging the head. In most cases, however, the pupil is round, although cats have a vertical slit-like opening in the iris, adapted to nocturnal explorations, while the seal has a curious pear-shaped pupil with the wide end next the nose.



Fig. 727. Umbraculum in the iris of a llama's eye. (After Plate.)

The lens in the mammalian eye is still less convex than that of reptiles or birds. It is more spherical in water forms and is relatively largest in nocturnal and crepuscular animals, such as bats, cats, and mice. Nocturnal animals are further characterized by the absence or paucity of color-receiving cones in the retina.

Detwiler says that "in mammals and man it is very questionable whether

pigment migration has been demonstrated definitely in any instance." He also doubts the occurrence of any contraction and elongation of rods and cones.

Stereoscopic perception of distance through triangulation resulting from binocular vision is especially essential to animals of prey. Among mammals it is present in some carnivora and in higher primates. It is also found in a few sharks and rays, toads, and carnivorous birds (e.g., hawks, owls, and some gulls). Lower vertebrates with lateral eyes and two fields of vision sacrifice the more accurate judgment of distance for a wider field of vision.

It should be remembered that a little more than half of the energy of extra-terrestrial light is appreciable to the photoreceptors of the human eye. About 43 per cent of the spectrum at the infrared end, and 5 per cent at the ultraviolet end, is "out of sight." The 52 per cent remaining, that is, between ether waves of 397 millionths of a millimeter in length at the violet end and 760 millionths of a millimeter in length at the red end, represents the entire output of photic energy for which the human retina is adequate. Within these extremely minute limits lies the whole visual splendor and variety of our color world.

VIII. INTERNAL SENSE ORGANS

Most of the sense organs thus far considered belong to the category of the *exteroceptors*, that is, sense organs adequate to receive stimuli arising outside of the organism. There are, however, sensations resulting in part at least from stimuli originating within the animal body, whose receptors are little known, but which nevertheless are functionally active. No doubt many of the generalized sensations, such as fatigue, nausea, "feeling fit" or "run down," lack specific sense organs, being the result of the general tone of several organs working together. The problematical receptors dealing with internal stimuli have been divided into *proprioceptors*, "located in the deeper regions of the body, stimulated only indirectly by environmental forces, but excited by processes within the organism itself" (Mitchell), and *interoceptors*, "located in the linings of the digestive system, and stimulated by conditions in this system."

1. Proprioceptors

These sense organs are closely related to pressure of some sort, acting (1) through muscles, tendons, and joints, as a "muscular sense," by means of which an idea of the weight of objects is gained, and the relative position of different parts of the body is realized; (2) through internal *nocireceptors*,

that give rise to warning rheumatic or visceral pains; or (3) through the semicircular canal apparatus, already described in connection with the ear, to secure equilibration and orientation in space.

The weight of any object is estimated by lifting, or "hefting" it, that is, testing by muscular resistance the pull of gravity which it exerts. For example it takes twice as much muscular effort to keep a ten-pound ball from falling when it has been lifted into the air as is necessary to sustain a five-pound ball in the same way. The difference in weight of the two balls is less accurately determined when they are simply placed in succession upon the hand while it rests upon a solid support without muscular exertion.

The kinaesthetic sense organs involved in the process of ascertaining the weight of objects are located not only in the muscles, but also in the tendons and joints. They are quite distinct from cutaneous sense organs of pressure that obviously supplement them in giving information about the character of ponderous objects.

2. Interoceptors

Appetite, hunger, and thirst are three distinct sensations associated with the digestive apparatus, for which adequate sense organs have not yet been discovered.

Appetite is a pleasant sensation, not to be confused with hunger, which is an unpleasant sensation. It has been described as the "memory of food enjoyment," brought about by internal changes in conjunction with such external stimuli as the sight, odor, or taste of food.

Hunger, which is sometimes erroneously referred to muscular contraction of the walls of an empty stomach, is the result of nutritional poverty in the blood, while the sensation of *thirst*, referred to the mucous lining of the throat, is due to an increase in the salt content of the blood, that impels the animal to replace if possible loss of water from the body. If hunger and thirst were pleasant sensations we would not be so concerned to banish them by food and drink.

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Index

Numbers refer to pages, those in bold face indicating pages on which the references include figures. The Bibliography is not indexed.

- A.*, 27
 Aard-vark, **71**, 72
 Abbervillian, 117, 118
 Abdomen, 5
 Abduction, 649
 Abomasum, 309
 Accommodation of eyes, 809, 817
Acerina, 462
 Acetabular bone, **618**
Acetabulum, 532, **607**, 608, 611, **612**, **613**, **614**
 Acheulian, 117, 118
 Acid, hydrochloric, 311
Acipenser, 34, 230, 290, 312, 560, 609, **610**
 Acraniota, 21
Acris, 43
 Aerodont, 293
 Acromegaly, 506
 Acromion, **621**
 Actin-, 33
Actinopterygii, 32, 33-35
Actinotrichia, 241, **609**, 619, 624
 Adam's apple, 423
 Adder, 51
 Amazon, 512
 Adduction, 649
 Adenase, 323
 Adenohypophysis, 504
 Adenoids, 304
 Adhesive organs (discs), 20
 Adrenal gland, 471, 509, 510
 Adrenalin, 510, 511, 750, 751
 Aestivation, 33
 Actiology, 182
Agama, 404
 AGASSIZ, 231, 702
 Age, Bronze, 115, **116**; Copper, 115, **116**; cultural, 115, **116**; of Fishes, 103; Ice, 104, 127; Iron, 115, **116**; of Mammals, 103; of Man, 99; Mesozoic, 45; of Reptiles, 103; Steel, 115; Stone, 115, 117
Agkistrodon, 51
 Aglossidae, 282
 Agnatha, 27
 Agraphia, 716
 Air, bladder—see bladder, swim; capillaries, **409**; complementary, 419; residual, 419; sacs, 387, **408-410**; securing of, 414-419; supplemental, 419; tidal, 419
 Aladdin's lamp, 600, 601
 Alar plate, 686, 687
 Albatross, 56
 Albino, 202, 811
 Albumen of egg, 159, 451, **452**
 Albumin, 223
Alces, 75
 Alexia, 716
 Algesireceptor, 759, 766, 767
 Alignment, 113
 Alisphenoid, 568, 570, 572, 573, 578, **580**
 Allantoic artery, 349, **351**; bladder, 438, 439; vein, 349, **351**
 Allantois, 44, 166, 318, **351**, 386, **486**
 Alligator, 43, **52**, 196, 233, 274, 282, 293, 407, 420, 452, 525, 536, 567, **576**, **613**
 ALLISON, 763
 Allosome, 138, 139
 Altricial, 247
Aluatto, 69
 Alveolus, 402, 405, **414**
Alytes, 38, 266, 473, 825
 Amber, 98, 100
Amblyrhynchus, 49
Amblystoma, 41, 396, 475, 549
 Ameloblast, 289, 290
Amin, 35, 230, 231, 406, 528, 560, 561
 Amino-acid, 327
Amiurur, 761, 780, 824
 Amniocoetes, 26, 267, 354, 463

- Ammodytes*, 268, 312, 461
 Amnion, 37, 43, 44, 486
 Amniotes, 44, 269, 318
Amoeba, 207, 265, 273, 329, 602, 672, 765
 Amoebic dysentery, 188
 Amphib, 22
Amphibamus, 40
 Amphibia, 17, 35-43
 Amphibian, amplexation, 473, 475; aortic loops (arches), 365-367; appendages, 603, 623, 625, 627; autonomic nervous system, 751; brain, 724, 727, 728; breathing, 416; care of young, 38; chromatophores, 217; development, 168-171; digestive system, 270, 272; ear, 788, 794, 803; egg, 451, 452; epidermal glands, 217; epithelial bodies, 502; eye, 824; fin, 623, 625; gills, 395, 396; heart, 355, 356; integument, 196, 210, 211, 212, 217; intestine, 312; jaws, 564; larynx, 421; lungs, 406; lymph hearts, 378; meninges, 699, 700; mesonephros, 445; mouth glands, 279; muscles, 654, 656, 660; nerve cord, 697; occipital condyles, 567; ovary, 461; pectoral girdle, 549, 550, 619, 620; pelvic girdle, 610, 611, 612; pharynx, 301, 302; respiration, 37, 200, 385; ribs, 545, 546; scales, 232; sense organs, 761, 769, 770, 774, 775, 777, 778, 781, 783; skull, 565-582, 569, 586, 587; sternum, 549, 550, 553; teeth, 293; thyroid gland, 500, 501; tongue, 281, 282; trachea, 403; urinary bladder, 438; urine, 436; urogenital ducts, 467, 468; veins, 372; vertebrae, 528, 529, 530, 532; voice, 420
 Amphicoelous, 527, 528, 329, 530
 Amphioxus, 21, 22, 23, 397; blood vessels, 342, 353, 369; development, 160, 176; digestive system, 273, 274, 280, 308, 318, 321, 499; excretory system, 440, 441; fins, 22, 23, 603; gills, 387-389; integument, 208; muscles, 630, 652, 654; nervous system, 683, 695, 696, 701, 702, 751; notochord, 525; reproductive system, 455, 466, 492; sense organs, 781, 802, 821; skeleton, 345, 603, 618, 623
 Amphiplatyan, 529, 531
Amphisbaena, 50
 Amphistylic, 564, 565
Amphiuma, 41, 334, 396, 406, 408, 548, 610
 Amplexation, 473
 Amplitude of vibrations, 801
 Ampulla, of Lorenzini, 769, 771; semicircular canal, 786, 787, 795, 796, 798; spermatie, 481
 Amylase, 327
 Amylopsin, 321, 323, 327
 An—, 583
Anabas, 386
 Anamnia, 44, 318
 Anaphase, 134, 135
 Anapsid, 583
Anas, 614
 Anatomy, comparative, 109
Anchitherium, 99
 Andr—, 463
Anguilla, 398, 492, 770
 Anguilliformes, 466
 Angular, 573, 576, 579, 581
 Animal, experimentation, 189; pole, 159, 160, 169
 Anisotropic bands, 154
 Ankle, 628, 636, 639, 640
 Annelid, 12, 273, 274, 341, 342, 440
Anofix, 50
 Anosmatic, 774
 Anseriformes, 56
 Antecater, 59, 70, 71, 250, 273; scaly, 70, 71, 213, 221, 233, 252; spiny, 59, 252, 476
 Antelope, 75, 220, 236, 477; pronghorn, 75, 236; saiga, 236
 Anterior, 8, 9
 Antihelix, 789
 Anthozoans, 273
 Anthrax, 187
 Anthropoidea, 68, 69
 Anthropology, 107, 109
Anthropopithecus, 69
 Antibody, 339
Antigonia, 28
Antilocapra, 75, 236
Antilopa, 75
 Antitoxin, 191
 Antitragus, 789
 Antivivisection, 190
 Antler, 234, 235
 Astrum of Highmore (maxillary sinus), 570, 594, 595, 819
 Anura, 38, 39, 42-43, 366, 416, 470, 530
 Anus, 6, 324, 325, 489, 490
 Anvil, 582
 Aorta, dorsal, 342, 343, 348, 350, 351, 361, 364, 365, 369, 471; pulmonary, 358, 361, 366, 367, 368; systemic, 358, 366, 367, 368, ventral, 342, 343, 348, 351, 354, 355, 363, 364, 365, 369
 Aortic arches (loops), 350, 351, 364-368; bodies of Zuckerkandl, 510
 Ape, 67, 69, 255, 256, 276, 285, 316, 425, 431, 478, 480, 693; claws, 237
 Ape-man, 120-122
 Aperture, mouth, 274
 Aphasia, 716

- Aphemia, 716
 Apoda—see gymnophiona
 Apophysis, 523
 Apparatus, hyobranchial, 283, 284, 571, 572, 576; hyoid, 571, 572; mammary, 224, 225, 226; voice, 420-426
 Appendage, 25; absence of, 604, 625, 626; evolution of, 634; lateral, 625; median, 603, 623; origin, 604, 605, 606; paired, 603, 623, 625; pectoral, 603; pelvic, 603; pentadactyl, 627; unpaired, 603, 623
 Appendicitis, 332
 Appendicularia, 21
 Appendix, epididymidis, 457, 487, 488; testis, 457, 468, 487, 488; vermiform, 269, 313
 Appetite, 831
 Apsid-, 583
 Apteris, 247
Apteryx, 55, 56, 410, 622, 626
 Aqueduct, Fallopian, 793; of Sylvius, 705, 706, 710
 Arachnoidea, 505, 698, 699
 Arbor vitae, 708, 709
 Arc, reflex, 670
Arca, 12, 333
 Arch, aortic, 350, 351, 364-368; of foot, 638, 639, 640; gill (branchial), 387, 394, 563, 572, 604; harnal, 522, 523, 527, 528, 532; hyoid, 563, 571, 572, 577, 659, 775, 789; mandibular, 281, 562, 573, 577, 659, 789; neural, 522, 525, 527, 528, 533; simple, 259; systemic, 357, 361; tented, 259; vertebral, 525; visceral, 572, 573, 577; zygomatic, 595
 Archææ, 54
 Archaeology, prehistoric, 107
Archaeopteryx, 54, 55, 238, 243, 290, 547, 554, 615, 630
 Archaeornithes, 54
 Archaeozoic, 102, 103
 Archerteron, 161, 163, 170, 171, 172, 174, 176
Archidiskodon, 299
 Archipallium, 712
 Archipterygium, 627
 Archisternum, 549, 554
 Arcuallia, 527, 528
 Area, of human skin, 202; olfactory—see lobe, olfactory; somesthetic (somesthetic), 716, 717, 719
 AREY, 439
 Argentea, 822
 Arginase, 323
 ARISTOPHANES, 422
 ARISTOTLE, 3, 97, 156, 380
 Arm, embryonic, 11; fore, 528; upper, 628
 Armadillo, 70, 71, 196, 213, 233, 252, 730
Aromochelys, 218
 Arrector pill muscle, 221, 251
 Arterial arches (loops), 350, 351, 364-368
 Artery, 341, 344, 345, 364-368; afferent branchial, 355, 365, 394, 395; allantoic, 349, 351; carotid, 350, 358, 365, 500; caudal, 351, 369, 522, 527; common carotid, 357, 541; cutaneous, 200, 357; efferent branchial, 365, 394, 395; external carotid, 365, 367, 368; hepatic, 317; interlobar, 435; interlobular, 433, 435; internal carotid, 365, 367, 368; intersegmental, 526; intestinal, 369; posterior thyroid, 502; pulmocutaneous, 357; pulmonary, 200, 343, 355, 357, 358, 361, 365, 367, 368, 406; renal, 431, 434; septal, 369; subclavian, 365, 367, 368, 500; umbilical, 349; vitelline, 173, 348, 350, 351, 364
 Arterioles, 341, 345
Arthroleptis, 38
 Articular, 564, 565, 570, 572, 573, 575, 576, 579, 581, 582
 Artifact, 100
 Artiodactyla, 62, 73-75, 77, 376, 637
 Artios, 72
 Arytenoid, 421, 422, 423, 425, 572, 577, 578
Ascaris, 455
 Ascidian, 18
 Askidion, 18
 Ass, 72
 Aster, 135
 Astragalus, 628, 638
Astrostopus, 663
Asymmetron, 21
Atelæ, 258, 480, 548, 641, 760
 Athlete's heart, 186
 Atlas, 534, 535
 Atrial cavity, 19, 23, 24, 389
 Atrichosis, 257
 Atriopore—see pore, atrial
 Atrium, of heart, 354, 355; of lung, 408
 Atrophy, 186
 Atropin, 750
Auchenia, 74, 253
 Auditory, center, 716, 717; nerve, 708, 713, 726, 734, 736, 737, 742, 797; pit, 791; sac, 791
 Auk, 57, 96
 Auricle, 355, 356, 363; left, 356, 359, 361; right, 356, 359, 361
 Aurignacian, 112, 118, 119, 125
 Autocoids, 497
 Autopsy, 188
 Autosomes, 138, 139
 Autostylic, 564
 Avebury, 114

- Aves, 17, 52-57
 Axis, 534, 535; skeletal, 522; visual, 807
 Axon, 666, 667, 669
 Azilian, 118
 Azygos system, 376

 Baboon, 69
 Backbone, 25, 537, 540
 Bacteria, 187
 Bacteriology, 188
 Badger, 64, 295
 Balaena, 79, 80, 242, 662
 Balanoptera, 79, 662
 Baldness, 257
 BALFOUR, 440, 814
 Bandicoot, 60, 478
 BANTING, 513
 Baptonodon, 290
 Barb, 243, 244
 Barbel, 391
 Barbule, of feathers, 243, 244; respiratory, 386
 Barbus, 211
 Barnacle, 215
 Barrier, 90
 Basal plate, 686, 687
 Basalia, 526, 605, 619, 624
 Basibranchial, 280, 283, 563, 576
 Basidorsal, 521, 526, 527, 528, 529, 532
 Basihyal, 280, 281, 283, 563, 568
 Basisoccipital, 566, 567, 568, 579, 580, 592
 Basipterygium, 606
 Basisphenoid, 567, 568, 577, 580
 Basiventral, 521, 526, 527, 528, 529
 Basophil, 336
 Bat, 58, 63; capillaries, 341; digestive system, 285, 292, 297, 307, 313; hearing, 790; integument, 201, 220, 222, 224, 239; nervous system, 677, 714; reproductive system, 478, 481, 492; wing skeleton, 630
 Batoides, 30
 Bdellostoma, 26, 27, 388, 390, 391, 442
 Beak, 242, 273, 276
 Bear, 65, 295, 297, 429, 430, 480, 481; brown, 64, 213, 233; cave, 124; marsupial, 61
 Beard, 253
 Beaver, 65, 67, 214, 222, 233, 294, 307
 Bell, A. G., 5
 BELL, SIR CHARLES, 684
 Belly of muscle, 646, 647
 Best, 513
 Bhudas, 291
 Bible, The, 16, 77, 251, 517
 Bile, 315; capillaries, 317; ducts, 305, 316, 319, 320; salts, 315
 Bion, 35
 Bird, air sacs, 387; aortic loops (arches), 367, 368; appendages, 630, 631, 634, 635; beak, 242, 273; brain, 725, 729; breathing, 417; breeding, 491; claw, 238; clitoris, 480; colic caeca, 269, 270; copulation, 473, 477; development of, 169-173; digestive system, 270, 272; ear, 788, 794, 803; egg, 159, 451, 452, 485; egg tooth, 300; epidermal glands, 218, 219; epiphysis (pinacal body), 507; esophagus, 304, 306; eye, 826, 827, 828; feathers, 243-249; fetal envelopes, 44, 486; hard palate, 302; heart, 355; integument, 201, 213, 218, 242; intestine, 312, 325; jaws, 564; locomotion, 519; lungs, 408, 409; lymph hearts, 379; meninges, 699, 700; mesonephros, 445; metanephros, 445; mouth glands, 276, 279; mouth opening, 274; muscles, 655, 656, 660; occipital condyle, 567, 589; ovary, 455, 461; parathyroid glands, 502; pectoral girdle, 622; pelvic girdle, 614, 615; penis, 477; ribs, 547; scales, 218, 233; sense organs, 774, 777, 778, 779, 781; skeleton, 518, 548; skull, 566-582, 589, 590; spurs, 242; sternum, 548, 551, 552; stomach, 307, 309; syrinx, 422, 423; teeth, 290; testis, 508; thymus gland, 503, 504; thyroid gland, 500; tongue, 283; trachea, 403, 404; urinary bladder, 438; urine, 436; urogenital ducts, 468, 469; veins, 375; vertebrae, 528, 530, 533, 534; voice, 420; wing, 548, 630
 Birth marks, 202
 BISCHOFF, 202
 Biron, 75, 112
 BISSENETTE, 491
 Bitter, 782
 Bivalve mollusk, 273
 BIZZORERO, 338
 BLACK, 122
 Bladder, air—see bladder, swim; allantoic, 438, 439; cloacal, 438, 439, 467; gall, 269, 306, 315, 316, 319, 320; pancreatic, 320; swim (air), 387, 397-401, 397-399, 462, 787; tubal, 437, 438; urinary, 269, 270, 434, 437-439, 457, 468, 476, 479, 481, 490
 BLAKESLEE, 783
 Blarina, 63
 Blastoderm, 452
 Blastomere, 160
 Blastopore, 161, 163, 170, 171; lip of, 170, 171, 179
 Blastula, 160, 168, 169
 Bleeders, 340
 BLES, 386
 Blind spot, 813, 814

- Blindness, 826
 Blood, 69, 142; amount of, 332; clot, 339; islands, 348, 349, 350; platelets, 336, 338; poisoning, 337; pressure, 506; Rh factor, 69; uses of, 330
 Blood cell, 132, 334, 336, 337, 350; formation of, 337, 348; number of, 334; red, 12, 132, 332-335, 336, 519; white, 132, 335-338, 336
 Blood vessels, of amphioxus, 342, 353, 369; of annelid, 341, 342; of fish, 343; of mammal, 343; tissues lacking, 341
 Blubber, 198, 199
 Boa constrictor, 408, 473, 626
 Boar, wild, 127, 297, 299
 Boas, 473
 Bobolink, 249
 Body, aortic of Zuckerkindl, 510; chromaffin, 510, 511; ciliary, 807, 809, 810; epithelial, 502; fat, 471; Golgi, 130; of hyoid, 577; lateral geniculate, 707, 733, 738, 739; mammillary, 708, 710, 711, 712, 713; Nissl, 569; parietal, 4, 507, 704, 705, 724, 728, 820; pineal, 499, 507, 705, 707, 708, 710, 711, 724, 728, 729, 820; pituitary—see hypophysis; reniform, 707, 710, 720, 721, 726, 727, 743; trapezoid, 713; ultimobranchial, 500, 502, 503, 504; vitreous, 807, 816; Wolffian, 443, 445, 456
 Bolk, 291
 Bombinator, 42, 609, 825
 Bone, 147-152, 148, 150; acetabular, 618; canaliculi, 149; cartilage, 150, 151; cells, 132; cheek, 595; chevron, 529; clitoris, 480; compact, 148, 149, 152; cotyloid, 618; dry, 517; ear, middle, 571, 791-794; endochondral, 151; fore arm, 628; hyoid, 424, 425; Inca, 591, 592; innominate, 615, 628; investing, 150, 561, 580, 581; as levers, 519; malar, 295, 555, 595; marrow, 148, 151, 152; marsupial, 617; membrane, 150; of operculum, 561, 564, 575; palm, 629; penis, 478; perichondral, 151; replacing, 150, 151, 561, 580, 581; sclerotic, 569, 827; sesamoid, 628, 633, 649; shank, 628; shoulder, 628; spongy, 148, 149, 152; sutural, 597; temporal, 555, 570, 582, 595; thigh, 628; tissue, 148-150; toe, 629; turbinate, 403, 569, 570; Wormian, 597; zygomatic, 595
 BORING, 509
 Bos, 75, 234
 Botryllus, 20
 BOUCHER DE PERTHES, 116
 Bowfin, 360
 Brachial patera, 633
 Brachiopods, 273
 Brachium, conjunctivum, 721; Brachium, pontis, 721
 Brachydactylism, 633
 Brachydont, 296
 Bradypus, 70, 71, 404, 534
 Brain, 695, 700-731; case, 555; comparative anatomy of, 723; compared with cord, 701; differentiation of, 703; flexures, 705; human, 707, 708, 710; sight, 703; smell, 703; stem, 701, 707, 710; ventricles, 705, 706, 707; weight of, 702
 Branch—, 41
 Branch (of nerves), 684; autonomic, 680, 683; branchial of Xth, 743; cochlear of VIIIth, 742, 797; cutaneous, 680, 780; deep ophthalmic of Vth, 726, 741; dorsal, 680, 683; hyomandibular of VIIth, 726, 742; infraorbital trunk of Vth and VIIth, 726; lateral of Xth, 726, 743; mandibular of Vth, 726, 741, 742; maxillary of Vth, 741, 742; meningeal, 680, 683; palatine of VIIIth, 726, 742; pharyngeal, 726, 737; postretrobulbar, 726, 737; pre-trematic, 726, 737; superficial ophthalmic of Vth and VIIth, 726, 741; ventral, 680, 683; vestibular of VIIIth, 742, 786, 797; visceral of Xth, 726, 743
 Branchiae, 387
 Branchial, 283, Branchial (gill) arch, 387, 394, 563, 572, 604
 Branchiostoma, 21
 BRAUS, 453
 Breast, 222, 223
 Breastbone—see sternum
 Breathing, 414-419; diaphragmatic, 418; pharyngeal, 10; by rectum, 386; rib, 418
 Breeding season, 491
 BREMER, 206, 449, 457, 676, 795
 Bristles, 252
 Brittle stars, 273
 Bronchioles, 401, 405
 Bronchus, 401, 405, 413, 414; recurrent, 409
 Brontomureti, 46
 BRUES, 765
 BRUNER, 374
 Bryozoans, 273
 Buccal cavity, 275, 276; cirri, 22; funnel (hood), 22, 209
 BUCKLAND, 97
 Bud, muscle, 605, 657; myotomic, 605, 657; taste, 780, 781
 Buffalo, 75
 Bufo, 42, 422, 530, 825
 Bulb, end, 568; hair, 250, 254; olfactory, 708, 712, 713, 725, 726, 733

- Bulbus arteriosus*, 355, 356
Bullfrog, 422
Bullhead, 307
Bundle, ground, 690, 695; of His, 363
Bunodont, 296
Bursa, of Fabricius, 270; of a joint, 521; omental, 328
Byarox-Oritz, 324

Cacops, 40, 611, 620
Caecilia, 40, 397, 443
Caecilians, 212, 232, 396, 548, 625
Caecum, 205; colic, 269, 270, 306, 312, 313; pyloric, 268, 269, 312
Caiman, 52
Caisson disease, 187
Calamoichthys, 230, 396, 397, 625
Calcaneus, 628, 638, 639, 640
Calcis, 628
Calcium metabolism, 503
Callichthys, 386
Calosity, 243
Caloreceptor, 759, 766, 768
Calvarium, 120
Calyx, renal, 431, 433
Cambrian, 103
Camel, 74, 242, 309, 334, 404, 473, 637
Camelus, 74
Campanula Halleri, 823
Canal (Meatus) auditory, external, 397, 788-791, 792, 803
Canal, central, 674, 675, 687, 688, 693, 696, 705, 706, 707, 710; cochlear, 797; haemal, 522, 523; ear, external, 397, 596; Haversian, 148, 149, 152; hyaloid, 816; inguinal, 459; invagination, 796; lateral-line, 769, 770; milk, 226; nasolacrimal, 818, 819; neural, 522; neurenteric, 163, 164, 674; pericardio-peritoneal, 177, 354; of Schlemm, 807, 816, 817; semicircular, 734, 742, 786, 787, 792, 795, 796, 798; urogenital, 437; uterovaginal, 488; vertebralarterial, 546, 547
Canaliculi, bile, 317; of bone, 149
Cancer, 185
Canis, 64, 65, 253
Cannon, 510
Capercaillie, 219
Capilla, 346
Capillary, air, 409; bile, 317; blood, 204, 341, 344-346, 347, 434, 486; rôle of, 346
Capitulum, 629, 632
Capitulum of rib, 522, 548
Capra, 75
Capsule, auditory—see capsule, otic; Bowman's, 432, 433, 434, 435, 443, 444; fibrous, 435; joint, 520; lens, 816, 817; nasal, 280, 565, olfactory, 556, 557-559, 569; optic, 556, 557, 568; otic, 556, 557-559, 564, 565, 568; sense organ, 556, 557; stroma, 334
Caput epididymidis, 469
Carapace, 48, 533, 547
Carbohydrate, 265, 314, 322, 323, 327; metabolism, 512
Carbon, dioxide, 384, 427; monoxide, 333, 774
Carboniferous, 103
Carcharias, 392
Cardiac, region of stomach, 307, 308
Care, parental, 454, 494; post-natal, 494; of young amphibians, 38
Caribou, 235
Carics, 300
Carina, 56, 404, 548, 551
Carinatae, 55-57
CARLSON, 336
Carn—, 65
Carnivora, 62, 64, 65, 66, 92
Carnivore, claw, 237; digestive system, 294, 295, 313, 318; integument, 222, 223, 225; kidney, 431; reproductive system, 478, 481; veins, 376
Carnivorous, 264
Carp, 35, 307, 334, 398
Carpal, 607, 627, 629, 632, 633
Carpale, 629, 632, 633
Cartilage, 132, 145, 146, 150; articular, 520; arytenoid, 421, 422, 423, 425, 572, 577, 578; basal, 605, 619, 624; basibranchial, 280, 283, 563, 576; basihyal, 280, 281, 283, 563, 568; calcified, 146; ceratobranchial, 280, 563, 576; ceratohyal, 280, 563, 565, 573, 576; cricoid, 421, 422, 423, 424, 425, 572, 577, 578; cuneiform, 424; ear, external, 572; elastic, 146; ensiform, 552; epibranchial, 280, 563; epicoracoid, 549, 550, 609, 620, 622; fibrous, 146; hyaline, 146; hyomandibular, 563, 565; hypobranchial, 280, 563, 576; hypohyal, 576; labial, 280, 565; laryngeal, 421-425, 571, 572, 577; lateral, 421; Meckel's, 280, 562, 565, 570, 572, 573, 578, 579; nasal, 594; palatoquadrate, 562; pharyngobranchial, 280, 563; pterygoquadrate, 280, 562, 564, 565, 572; radial, 605, 609, 619, 624; rostral, 585; of Santorini, 424; sclerotic, 568, 828; sternal, 549, 552; thyroid, 423, 424, 425, 571, 572, 577, 578; tracheal, 404, 421, 424, 571, 572; triticeous, 424; xiphoid, 552, 553; ypsiloid, 610, 611, 612
Carruncula lacrimalis, 819
Casarin, 311
Cassowary, 56

- Caster*, 67, 253, 294
Castration, 508
Cat, 65, 334, 420, 756; brain, 713; civet, 64, 222, 313, 618; digestive system, 278, 287, 297, 316, 320; integument, 220, 239, 250, 251, 253; reproductive system, 460, 477, 481; skeleton, 552, 577
Cata, 69
Catarrhine, 69, 297
Caterpillar, 266
Catfish, 35, 761, 780
Cattle, 75, 223, 256, 252, 274, 275, 286, 297, 309, 420, 493, 762
Cauda, epididymidia, 469; equina, 681, 682
Caudata—see *urodela*
Cavern, 236
Cavia, 65
Gaviar, 34
Cavity, atrial, 19, 23, 24, 389; buccal, 275, 276; coelomic—see *coelom*; ear, middle, 397, 567; endovarian, 462; glenoid, 549, 550, 607, 608, 609, 619, 621, 622; greater peritoneal, 430; joint, 520; lesser peritoneal, 430; marrow, 148, 151, 152; nasal, 303, 401, 403, 412, 778; oral, 275, 277, 303, 401; orbital, 280, 574, 578, 579, 587; ovarian, 462; pericardial, 177, 178, 353; perilymphatic, 792, 798; peritoneal, 177, 178, 354, 430; pleural, 177, 178, 413; pleuroperitoneal, 177; pulp, 287, 288, 289; segmentation, 160, 161, 164, 168, 169, 170, 176, 178; thoracic, 178; true body, 9; tympanic, 792, 793, 794, 798
Cebus, 68
Cell, 129; acidophil, 506; amacrine, 812, 814; basal, 776, 777; basophil, 506; beaker, 209, 216; blood, 132, 334, 336, 337, 350; body of, 130; bone, 132; cartilage, 132, 146; chromaffin, 510, 751; chromophob, 506; of *Claudius*, 799, 800; commissure, 696; cone, 808, 811, 812; Deiter's, 799; differentiation of, 131; endothelial, 341, 348, 350; ependymal, 685, 686, 696; epithelial, 132, 271; ethmoidal, 570, 593; fat, 132; flame, 428, 441; follicular, 159; ganglionic, of retina, 811, 812; generalized tissue, 130; germ, 157, 455, 458; germinal, 685, 686; goblet, 271; granular gland, 209, 216; haemopoietic, 348; hair, 769, 780, 786, 787, 799, 800; Hensen's, 799, 800; intermediate, of retina, 811; interstitial, 458, 508; liver, 317; lutein, 465, 509; Malpighian, 203; mastoid, 596, 791; membrane, 130; muscle, 132, 152, 154, 205, 645, 671; nerve, 132, 154, 666; neuroglia, 155, 666, 685, 686, 812; notochordal, 524; olfactory, 776, 777; phalangeal—see also *cell*, Deiter's, 800; photoreceptive, 805, 821; pigment, 205, 210; pillar, 799, 800; polar, 136; Purkinje, 709; pyramidal, 720; red blood, 12, 132, 332-335, 336, 519; Rouget muscle, 347, 348; sensory, 776, 777; Sertoli, 458; sex, 157, 455, 458; sperm, 132, 136, 449-451, 449, 458, 472; spindle, 338; stimulator, 762, 763; sustentacular, 458, 776, 780; theory, 129; types of, 132; water, 309; white blood, 132, 335-338, 336
Cell-mass, inner, 174
Cellulae aëreae, 408
Cellulose, 208
Cement, 288, 289
Genozoic, 103, 127
Center, 676; association, 700; auditory, 716, 717; coordination, 701; correlation, 701; cortical, 715, 716, 717; hearing, 716, 717; motor, 701, 716, 717, 722; olfactory, 716, 773; organization, 178; reflex, 670; sensory, 716, 717; sight, 716, 717; somesthetic (somatæsthetic), 716, 717, 719; speech, 716; visual, 716, 717
Centrale, 627, 629, 632
Centriole, 130, 135
Centrosome, 130, 134
Centrum, 522, 523, 527, 533, 541; amphicoelous, 527, 529; amphiplatyan, 529; chordal, 528; heterocoelous, 529; opisthocelous, 529; perichordal, 528; procoelous, 529
Cephalochordata, 17, 21-25
Cephalon, 32
Cephalophus, 220
Ceratobranchial, 280, 563, 576
Ceratohyal, 280, 563, 565, 568, 573, 576, 577
Ceratophora, 234
Cercopithecus, 253, 285
Cerebellum, 692, 701, 704, 708, 709, 710, 714, 721, 723-726, 727-729, 730
Cerebrum, 693, 701, 704, 714, 715, 716, 717
Ceros, 72
Cervidae, 234
Cervix of uterus, 479, 481, 483
Cetacea, 62, 78-80, 92, 220, 221, 224, 412, 477, 478, 481, 625
Chaetodon, 28
Chain, sympathetic nerve, 681
Chalaza, 452
Chalones, 497
Chamber, anterior of eye, 807, 816, 817,

- 818; anterior of swim bladder, 398, 399;
branchial, 392; nasal, 401, 403, 412;
posterior of eye, 807, 816, 817, 818;
posterior of swim bladder, 398, 399;
vitreous, 816
- Chameleon*, 50, 234, 828
- Chameleon*, 50, 234, 282, 283, 408, 412
- Chamois*, 127
- Charadriiformes*, 57
- Chauliodus*, 216
- Check, 274; bone, 595; pouch, 276
- Cheetah*, 65
- Chellean*, 117
- Chelonia*, 49
- Chelonia*, 48, 49, 290
- Chelydra*, 48, 49
- Chenocentrus*, 312
- Chevron bone, 529
- Chevrolet*, 74
- Chewing*, 274
- Chiasma*, optic, 704, 708, 711, 723, 724,
738, 739; pharyngeal, 302, 303, 304
- Chiasmatic groove*, 570
- Chick, development of, 169-172, 173, 349,
350, 775
- Chimæra*, 32, 769
- Chimpanzee*, 69, 125, 126, 544, 639
- Chin, angle, 599, 600
- Chiro-*, 63
- Chiroptera*, 62, 63, 92
- Chirose*, 625
- Chitin*, 207
- Chlamydoselachus*, 392, 393
- Chlorophyll*, 600, 601
- Choana*, 302, 416, 778
- Cholera*, 187
- Chaloeus*, 70, 221, 534, 547
- Chondr-*, 29
- Chondrichthyes*, 29-32
- Chondriosome*, 130
- Chondroblast*, 146
- Chondroclast*, 151
- Chondrostel*, 34, 393
- Chorda tendinea*, 360, 361
- Chorda tympani*, 742
- Chordata* (*Chordates*), 9, 12, 16
- Chordates*, borderline, 17; characteristics,
9-12
- Chorion*, 44, 486
- Choroid*, 807, 809, 810
- Chorology*, 82, 109
- Chorus*, 82
- Chromaffinoblast*, 510
- Chromatin*, 130, 134, 135
- Chromatophore*, 217, 671
- Chromosomes*, 130, 133, 134, 135, 139;
reduction of, 464; sex, 138, 139
- Chronometers*, archaeological, 110
- Chrysemys*, 49
- Chrysocloris*, 62, 221, 298
- Chrysophrys*, 463
- Chyle*, 314, 324, 327
- Chyme*, 308, 322, 327
- Cicero*, 27
- Ciconiiformes*, 56
- Cilia*, 200, 273, 308
- Ciliary*, body, 807, 809, 810; muscle, 740,
807, 810, 817, 818
- Ciliated fraternity*, 273
- Cillum*, 220, 818
- Circulation*, allantoic, 349; of amphioxus,
342, 369; of annelid, 341, 342; of fish,
343; of mammal, 343; systemic, 349;
vitelline, 349, 350
- Cirri*, buccal, 22
- Cladoselache*, 29, 30
- Cladoselachii*, 29
- Clarias*, 386
- Clark*, 686, 694, 716, 717
- Clasper*, 474, 475
- Clasas*, 14
- Classification*, 13
- Clavellus*, 390
- Clavicle*, 404, 541, 550, 608, 609, 618, 619,
620-622, 623, 628
- Claw*, 237-239, 613
- Cleavage*, 160, 168, 169, 174
- Cleft*, hypophyseal, 505; visceral, 388
- Cleithrum*, 575, 619, 620, 621
- Clinic*, 188
- Clitellum*, 215
- Clitoris*, 478, 480, 490; bone, 480
- Cloaca*, 166, 325, 437, 438, 446, 466, 467,
468, 471, 476, 478, 479
- Clot*, blood, 339
- Cnidaria*, 215
- Coagulase*, 327
- Cobitis*, 386, 462
- Coccyx*, 535, 537
- Cochlea*, 742, 791, 798, 804
- Codfish*, 35, 453, 463, 536, 603
- Coel-*, 528
- Coelenterata*, 215, 273
- Coelogenys*, 253
- Coelom*, 9, 23, 162, 164, 165, 172, 178
- Cornolestes*, 60
- Cold*, 692
- Cold-bloodedness*, 331, 334
- Colic caecum*, 269, 270, 306, 312, 313
- Collar* of hemichordate, 17
- Collateral*, 666, 667, 669; recurrent, 709
- Colliculus*, anterior (superior), 707, 708,
710, 733, 738, 739, 740; posterior (in-
ferior), 707, 708, 710, 743; scissuralis,
487, 488
- Colon*, 305, 324

- Coloration, protective, 197, 273; warning, 197
- Coluber*, 51
- Columba*, 589
- Columnella*, 571, 572, 581, 582, 587, 794
- Column, of Bertini, 431, 434; Clarke's, 687, 691, 720; dorsal, 689, 690, 718, 719; lateral, 687, 745, 746; somatic motor, 727; somatic sensory, 727; vertebral, 25, 521, 537; visceral motor, 727; visceral sensory, 727
- Colus*, 236
- Colymbiformes*, 56
- Commissure, anterior, 704, 708, 713, 725; dorsal, 687, 688; habenuar, 707, 710, 711, 724; posterior, 507, 704, 710; ventral, 687, 688, 719, 720; white, 692, 693, 694
- Component, nervous, 687, 737
- Composite finger tip, 259
- Concha, ear, 789; nasal, 569, 570, 776, 779, 819
- Concrescence, 298
- Condor, 56, 96
- Condyle, mandibular, 598; occipital, 534, 558, 559, 566, 567, 587, 589, 592
- Condylura*, 63, 292
- Cone, 808, 811, 812
- Coney, 77, 285
- Conger eel, 334
- Congo snake, 41
- Conjunctiva, 202, 807, 817; bulbi, 818; palpebrarum, 818
- Conadactes*, 578
- Constriction, of brain, 703; muscular, 649
- Contractility, 643
- Conus arteriosus, 354-357, 363
- Convolution of cerebrum, 714
- Convulsion, 503
- Coördination, chemical, 497; nervous, 497, 701, 709, 720
- COPE, 298
- COPENHAGEN, 763, 807, 812
- Copperhead, 51
- Coprolites, 100, 312
- Copula, 283, 285
- Copulation, 158, 472, 473, 475, 477
- Coraciformes*, 57
- Coracoid, 404, 548-550, 575, 607, 608, 609, 618, 619-622, 628
- Coracoscapula, 549, 619, 620
- Coral, 265
- Cord, human, 677; junctional, 469; nerve, 12, 20, 144, 164, 178, 267, 442, 522, 677-688; Pflüger's, 465; spermatic, 459; spinal, 178; vocal, 303, 422, 424, 425
- Coregonus*, 290
- Corium, 195, 203, 204, 205, 206
- Cormorant, 56, 828
- Cornea, 569, 807, 809, 817, 818
- CORNER, 494
- Corneum, 203, 204, 205
- Corona radiata*, 159
- Coronoid, 576, 579, 581
- Corpora quadrigemina, 701, 710, 725, 728, 730
- Corpus, albicans, 465; callosum, 708, 713, 729; cavernosum, 476, 477, 480, 481, 490; hæmorrhagicum, 465; luteum, 465, 495, 509; spongiosum, 476, 477, 480, 490; striatum, 704, 712, 723, 724, 725, 727, 728, 729
- Corpuscle, Grandry, 763; Herbst, 763; Meissner, 762, 763; Merkel, 762; red blood, 334, 336, 519; renal, 432; Vater-Pacinian, 762, 763
- Correlation, 701
- Cortex, of adrenals, 510, 511; cerebellar, 709; cerebral, 692, 712, 715, 716, 717, 722, 728, 729; of hair, 250; of ovary, 463; renal, 431, 434, 435
- Coati, 799
- Cortin, 512
- Costal facet, 523; plate, 533
- Cotyloid, 618
- Cotylomur, 45, 47, 567, 578, 621
- Cow—see cattle
- Coyote, 65
- Craniata, 17, 25-30
- Craniostylic, 564, 565
- Cranium, 25
- Crest, neural, 674, 675
- Cretaceous, 103
- Cretin, 501
- Cribriform, 569, 570, 593
- Cribrum, 593
- Cricetus*, 481
- Cricket, 765
- Cricoid, 421, 422, 423, 424, 425, 572, 577, 578
- Crista, ampullaris, 786, 796; galli, 570, 582, 592
- Crocodile, circulatory system, 358, 359, 375; digestive system, 293, 300, 319; gastralia, 554; reproductive system, 451, 461, 475, 476, 480; respiratory system, 403, 408; scales, 233; urinary bladder, 438
- Crocodylia, 48, 52
- Crocota*, 64
- Cro-Magnon, 112, 119, 125, 126, 127
- Cronlech, 113
- Crop, 306
- CROSSER, 687, 696, 697, 821
- Croisopterygii, 32
- Crotalus*, 51, 52, 242
- CROTHERS, 85

- Crown, of tooth, 287
Crus cerebri, 707, 710, 711, 720, 721
 Crustacean, 196, 498
 Crypt of Lieberkühn, 314, 322
Cryptobranchius, 41, 396, 610, 627
Cryptorchium, 460
Cryptos, 460
Cuboidrum, 629
 Cuckoo, 57
Cuculiformes, 57
 Cud chewing, 74, 309
 Cuneiform, 424, 628, 629, 638
 Cup, corneal, 245; optic, 705, 808, 814; pigment, 806, 821
 Curvature, greater of stomach, 307, 308; lesser of stomach, 307, 308; spinal, 538
 CUSHING, 506
 CUSHMAN, 5
 Cusp, 298
 Cuticle, 207, 208; of hair, 250
 Cutting the teeth, 289, 290, 292
 Cuvier, 120, 702
 Cycle, menstrual, 495; oestrous, 493
 Cycle-, 25
Cyclopes, 70
Cyclostomata, 17, 25, 26, 27
Cyclostome, 397, 545, 618, 625; autonomic nervous system, 751; axial skeleton, 525, 532, 584; brain, 723; branchial arteries, 364; fin, 623; gills, 390, 391; horny teeth, 209, 290; integument, 209; intestine, 268, 308, 312; mouth, 274; muscles, 654; nerve cord, 695, 696; sense organs, 769, 787, 802, 820, 821; spinal nerves, 683; tongue, 280
Cynaesturus, 65
Cynognathus, 45
Cynomyi, 67
Cynoscion, 400, 401
Cyprinidae, 400
 Cyt-, 338
 Cytology, 129
 Cytomorphosis, 130, 131
 Cytoplasm, 130
 Cytosome, 130

 Dactyl-, 72, 627
 Dactyloscopy, 260
 DAGUERR, 5
 DAHLGREN, 146
 DANA, 336
 Dandruff, 204
 DANTE, 304
 DARWIN, 15, 661
 Darwin's point, 789
Dasyprocta, 253
Dasyurus, 70, 71, 313
Dasyurus, 61

 DAVENPORT, 301, 506, 765
 Dawn men, 124
 DAWSON, 123, 124
 Deaminase, 323
 DEAN, 26
 Death, 261
 DEBEER, 684
 DECUS-, 709
 Decussation, of pyramids, 708, 709, 710, 720, 722; sensory, 718, 719
 Deer, 58, 74, 75, 220, 234, 637; musk, 222
 Degeneration, Wallerian, 689
 Delamination, 10, 674
Delphinus, 79
 Demibranch, 391, 392, 394
 Dendrite, 155, 666, 667, 669
Dendrohyrax, 77
 Dental, formula, 297; lamina, 288, 289
 Dentary, 565, 568, 575, 576, 579, 581, 582
 Dentine, 287, 288, 289
 Dentition, definitive, 291; milk (lacteal), 291; prelacteal, 291; post-definitive, 291
 Depression, 649
 Derm, 27
 Derma, 167, 195, 203, 204, 205, 206
 Dermatome, 165
Dermochelys, 48
 Dermo-occipital, 578
 Dermoptera, 62, 63, 92
 Derotremata, 396
 DESCARTES, 508
 Desiccation, protection against, 36
Desmodus, 309
 DETWILER, 824, 827, 829
 Development, of amphibians, 168-171; of amphioxus, 160, 176; of birds, 169-172, 173; of heart, 352, 353; of mammals, 173, 174, 175; of reptiles, 169-173
 Devonian, 103
 Di, 33
 Diabetes, 512
Diadectes, 621
 Diagnosis, clinical, 332
 Diapedesis, 337, 344
 Diaphragm, 177, 178, 418, 419, 647, 648, 657
 Diaphragmatic breathing, 418
 Diaphysis, of bone, 151
 Diapophysis, 522, 523, 546
 Diapsid, 583
 Diarthrosis, 520
 Diastema, 294, 297
Dicynodon, 621
Didelphys, 60, 61, 222, 224, 298, 445, 478, 479
 Diencephalon, 703, 704, 705, 711
 Differentiation, 160, 298
 Digestion, essentials of, 326, 327

- Digestive, enzymes, 276, 321, 323, 326, 327; sac, 265; surface, 266; tube, 263, 322; tube, formation of, 166; tube, length of, 268
- Digit, 606
- Digital, pad, 237; tips, 237; tori, 258
- Digitigrade, 637
- Dilatator pupillae, 811, 817
- Dilation, 649
- Dinoceras*, 234
- Dinornis*, 56
- Dinosaur, 46, 47, 530, 677, 678
- Dinotherium*, 76
- Diocoel, 705
- Diocious, 463
- Diphtheria, 188, 191
- Diphycercal, 624
- Diphyodont, 291
- Diplocaulus*, 40
- Diplosocus*, 46
- Dipnoi, 32, 33, 231, 268, 312, 356, 396, 406, 438, 525, 532, 564
- Dipus*, 67
- Disc, adhesive, 20; germinal, 159; intervertebral, 523, 528, 529, 539; optic, 814; sucking, 217
- Disease, 183; Addison's, 512; bacterial, 187; caisson, 187; control of, 191; Graves', 501; protozoan, 188
- Dispersal, 86, 89
- Distribution, laws of, 83
- Disturbances, 184
- Diuretic, 200
- Diverticulum, liver, 24; supplementary, 268
- Division of labor, 160, 272
- Dodo, 96
- Dog, 65, 334, 420, 481, 756; hard palate, 277, 278; integument, 222, 239, 251, 256; liver, 316, 318; prairie, 66, 67; stomach, 311; teeth, 295, 297, 298; tongue, 285, 287; vertebrae, 536
- Dogfish, 4, 30, 31, 229, 291, 367, 392, 474, 475, 769
- DOLBEAR, 765
- Dolichoglossus*, 17, 18
- Dolichonyx*, 249
- DÖLLINGER, 702
- Dolmen, 113
- Dolphin, 79, 290, 295, 598
- DONALDSON, 676
- Donsky, 239, 420, 424
- Doras*, 386
- Dorsal, 7, 8
- Dorsum of tongue, 232
- Dove, 57
- Draco*, 49, 201
- Dragon, 50
- Dromedary, 74, 242
- Drumfish, 400, 420
- DUBOIS, 120
- Duck, 56, 201, 219, 404, 422, 477, 614, 763
- Duckbill, 59, 276, 463
- Duct, accessory Wolffian, 474; of Bellini, 433; bile, 305, 316, 319, 320; of Botalli, 366; choledochal—see ductus choledochus; cochlear, 792, 795, 796, 797, 798; of Cuvier—see vein, common cardinal; cystic, 316, 319, 320; ejaculatory, 457, 470, 481, 488; endolymphatic, 786, 791, 795, 796, 797, 798; Gaertner's, 468, 487, 488; genital, 467, 468; hepatic, 316, 319, 320; lacrimal, 403, 818, 819; liver, 305, 316, 319, 320; longitudinal of testis, 467; lymphatic, 580; mammary, 223, 226; mesonephric—see duct, Wolffian; Müllerian, 455, 457, 467, 468, 470, 471, 480, 487, 488; (canal), nasolacrimal, 818, 819; pancreatic, 316; papillary, 433, 435; pneumatic, 398, 399; pronephric, 442; Rathke's, 468; of Rivinus, 278; salivary, 276; of Santorini, 319; segmental, 442, 445, 466, 467, 468, 470; sperm, 458, 469, 476; Stenson's, 276; sublingual, 276; thoracic, 314, 380; thyroglossal, 281, 283, 285; urinary, 436, 437, 438, 466, 468, 476; urogenital, 437, 467, 468, 470, 476; utriculo-saccular, 797; Wharton's, 276, 278, 279; Wirmung's, 319, 320; Wolffian, 318, 444, 445, 446, 455, 462, 467, 468, 469, 470, 471, 474, 487
- Ductulus, aberrans, 457, 487; efferens, 457, 458, 468, 469
- Ductus, arteriosus, 366, 367; Botalli, 366; choledochus, 316; deferens, 437, 457, 458, 459, 468, 469, 470, 476, 481, 487, 488, 490; epididymidis, 457, 469, 487; reunions, 796, 797, 798
- Dugong, 78, 299
- Duodenum, 305, 313, 315, 316
- Dura mater, 505, 698, 699
- Dwarfism, 185, 506
- Eagle, 56
- Ear, brain, 703; capsule, 556, 557-559, 564, 565, 568; development, 791; drum, 397, 579, 791, 803; external, 734, 788-791; external, canal, 397, 596; external, cartilage, 572; internal, 788, 795-804; lobule, 789; lop, 790; middle, 788, 791-795; middle, bones, 571, 791-794; middle, cavity, 397, 567; muscles, 662, 663, 790
- Earth, habitable, 108
- Earthwork, 114
- Earthworm, 207, 215, 440, 671
- Easter Island, 114
- Ecdysis, 207, 210, 233, 238, 246, 257, 374

- Echidna*, 58, 59, 220, 226, 227, 431, 445
Echinoderm, 18, 265
Ecology, 82
Ectethmoid, 569, 580
Ectocuneiform, 629
Ectoderm, 161, 162, 163, 164, 167, 170, 171, 172, 174, 175, 206
Ectopterygoid, 575, 576
Ectosarc, 207
Edentata, 62, 70-71, 71, 92, 285, 313, 376, 730
El, 35, 229, 394, 398, 492, 770; conger, 334, 777
Effector, 670; independent, 672
Egg, 156, 157, 449, 451, 452, 453, 454, 460, 465, 472, 495; abortive, 136; albumen of, 159, 451, 452; amphibian, 158, 451, 452; amphioxus, 158; Apteryx, 159; birds, 159, 451, 452, 485; case, 453; cleavage of, 160, 168, 169; fertilized, 156, 448, 463; fish, 158, 453; frog, 451; human, 159; implantation of, 495; kinds of, 158; mammal, 158, 453, 454; of mon, 159; ostrich, 159; reptile, 159, 452-454; segmentation of, 160, 168, 169; shell, 451, 452, 453, 485; telolecithal, 168; tooth, 300; white of, 451
Elassobranch, circulatory system, 356, 370, 371; digestive system, 268, 270, 312; reproductive system, 453, 460, 461, 470, 484, 485; respiratory system, 392, 393, 397; skull, 585
Elassobranchii, 29, 30, 31
Elastica externa, 524
Electrophorus, 663, 664
Electroplax, 664
Eleidin, 204
Elephant, 73, 76, 334, 420, 425, 492, 518; brain, 702; digestive system, 294, 296, 297, 299; integument, 222, 223, 239, 249; trunk, 76, 274, 776
Elephas, 76
Elevation, 649
Elk, 75; Irish, 235
Embolus, 340
Embryology, 156, 167; experimental, 157
Embryonic, plate, 174, 175; shield, 175
Eminence, genital, 490
EMPHYOCLES, 97
Emu, 56
Emulsification, 327
Enamel, 287, 288, 389; organ, 288, 289
Encephalon, 703
End bulb, 668; bulb, Krause, 762, 767
Ending, Ruffini, 767
Endocardium, 332, 353
Endocrine, 143
Endocrinology, 498
Endoderm, 161, 162, 163, 164, 167, 170, 171, 172, 174, 175
Endolymph, 377, 787, 795, 798
Endoneurium, 676
Endopterygoid, 575, 576
Enderachis, 698, 699
Endosarc, 207
Endostrium, 698
Endostyle, 19, 23, 24, 26, 390, 499
Endothelial cells, 341, 348, 350
Endothelium, 405
Endovarian cavity, 462
Enterocoele, 176
Enterokinase, 322, 323, 327
Entocuneiform, 629
Entoderm—see *endoderm*
Entoglossal, 571, 576
Entomostracan, 273
Envelope, fetal, 44, 486
Enzyme, 276, 321, 323, 326, 327, 339
Eoanthropus, 124
Eohippus, 73, 99, 100, 638
Eolith, 117
Eolithic, 117
Eosinophil, 336
Epaxial, 178
Ep(i), 206
Ependyma, 685, 686, 696
Epibranchial, 280, 563
Epicardium, 353
Epicoracoid, 549, 550, 609, 620, 622
Epicrinium, 456
Epidermis, 167, 195, 203, 206
Epididymis, 456, 457, 459, 467, 468, 469, 474, 481, 487, 488; caput of, 469; cauda of, 469
Epiglottis, 282, 302, 303, 423, 425, 571, 572, 735
Epihippus, 99
Epihyal, 568, 577
Epimere, 164, 167, 168, 349
Epimysium, 649
Epinephrin, 510
Epineurium, 676
Epiotic, 568, 580
Epiphysis, of bone, 151, 529; of brain, 507, 704, 705, 723, 724, 725, 726-729
Epipterygoid, 570, 574, 580
Epipubis, 610
Epithalamus, 507, 711
Epithelial cells, 132, 271
Epithelium, 142; ciliated, 142; columnar, 142, 143; cuboidal (cubical), 142; pigment of iris, 811, 817; pigment, of retina, 812; respiratory, 405; squamous, 142; stratified, 142, 143
Epitrichium, 206, 254
Epitympanum, 791

- Eponychium*, 240, 241
Epoöphoron, 468, 479, 487, 488
Equilibrium, 709, 784
Equus, 72, 73, 99
Era, Archæozoic, 102, 103; Cenozoic, 102; geologic, 102, 103; Mesozoic, 103; Palæozoic, 103; Proterozoic, 102, 103
Erepace, 327
Erepsin, 322, 323, 327
Erethizon, 67
Eriulus, 253
Erimæus, 63, 213, 481, 660
Ermine, 65
Eruption of teeth, 289, 290, 292
Eryops, 40, 547
Erythrocyte, 12, 132, 332-335, 336, 519
Esophagus, 303, 304-306, 305, 541, 735
Esox, 398, 438
Eutrogen, 509
Ethmoid, 568, 569, 570, 575, 582
Ethmoidal cells, 570, 593
Ethnology, 109
Eu, 60
Eumelotias, 66
Eurycea, 281, 282, 283, 407, 438
Eustachius, 509
Eutheria, 58, 60-80
Evagination, 704, 711
Excretion, 143, 200, 427
Exoccipital, 566, 567, 568, 580, 587, 592
Exocoetes, 386
Exocrines, 143
Exoskeleton, 12, 196, 207
Expansion, 84, 85
Experimentation, animal, 189
Expiration, 415, 418, 419
Extension, 649
Extroceptor, 758, 759
Extra-columella, 794
Eye, accommodation of, 809, 817; autonomic innervation, 751; brain, 703; camera, 806; color, 811; comparative anatomy, 821; direction, 805, 806; epiphyseal, 820; human, 806, 807; image-forming, 805, 806; median, 728, 820; mosaic, 806; parietal, 820; pineal, 820; telescopic, 822
Eyelash, 818
Eyelid, 817, 818, 819, 822
Face, 274, 275
Facet, costal, 523
Factor, barometric, 187; biological, 187; chemical, 187; mechanical, 187; Rh, 69; thermal, 187
Falconiformes, 56
Family, 14
Fang, 279, 300, 588
Fascia, 145; lata, 655
Fasciculus, 649, 688; corticospinalis (cerebrospinalis), 691, 718; cuneatus, 689, 691, 692, 719, 721; gracilis, 689, 691, 692, 718, 719, 721; proprius, 690, 691, 693, 694
Fat, 197, 203, 205, 265, 314, 323, 324, 327; body, 471; cells, 132
Fatigue, 644
Fauces, 277, 304
Feather, 243-249, 243-245, 247; color of, 248; contour, 245; developing, 243, 244, 245; hooks, 243, 244; lay of, 248; nestling down, 245; pattern, 249; periderm, 244; pin, 245, 246; powder down, 245; quill, 243, 245; shaft of, 243, 244; tail, 245; tracts, 247; vane, 243; wing, 245
Feces, 327
Feeder, sedentary, 273
Feeler, 253
Felis, 15, 64, 65
Femur, 607, 613, 628
Fenestra, 550; cochlear, 799; hypophyseal, 557, 559; ovalis, 792, 793, 799; rotunda, 792, 798, 799; tympani, 799; vestibuli, 799
Fertilization, 136-138, 137, 157, 472; internal, 475
Fiber, 67; Müller's, 696, 697; muscle, 132; myelinated, 669; nerve, 666; postganglionic, 745-749; preganglionic, 745-749; Remak's, 668, 669; spindle, 134, 135; supporting of Müller, 814; unmyelinated, 669; zonular of Zinn, 816
Fibrin, 339
Fibrinogen, 339
Fibula, 607, 628
Fibulare, 627, 628
Field, 100
Field, glandular, 281, 285; milk, 225, 226
Fila olfactoria, 738
Filament, gill, 388
Filum terminale, 677, 682
Fimbriae, 479
Fin, of amphioxus, 22, 23, 603; anal, 623; caudal, 603, 623, 624; dorsal, 603, 623; fold, 23, 604, 605, 606; median, 23, 603, 605, 623; paired, 603, 605; pectoral, 603, 605; pelvic, 474, 603, 605; rays, 609, 619; spine, 624; unpaired, 603, 623; ventral, 603, 623
Finger, 629; prints, 259, 260
Fish, 27-35, 305, 338, 548; aortic loops (arches), 365; autonomic nervous system, 751; bony, 32-35, 321, 372; brain, 723, 725, 726, 727; breeding, 452, 475, 491, 492; brood sacs, 485; cartilaginous, 29-32, 527, 697; circulatory plan of,

- 343; deep sea, 822; digestive system, 268, 269, 272, 273, 279, 280, 290, 292, 293, 294, 301, 302, 307, 312, 321; ear, 802, 803; eggs, 158, 453; electric, 653; elephant, 31; endocrine glands, 500, 503, 507, 511, 513; eye, 820-824; fins, 603, 619, 623, 624, 625, 626, 627; ganoid, 268; gills, 391, 392-395; gonads, 456, 460, 461, 462, 463, 467; gristle, 30; heart, 355, 356; integument, 196, 211, 216, 217, 229-232, 241; jaws, 564, 565; lobe-finned, 32; locomotion, 29, 201, 519; meninges, 699; muscles, 656, 658, 660; nerve cord, 697; occipital condyle, 567; pectoral girdle, 618, 619; pelvic girdle, 609, 610; physoclistous, 398; physostomous, 398; ray-finned, 33; respiratory organs, 386, 387, 391-401, 415; ribs, 542, 545; sense organs, 761, 768, 769-771, 774, 775, 777, 778, 780, 781, 787; skull, 560, 561, 566-582, 575, 585; sound production, 420; spinal nerves, 683, 684; spook, 31; swim (air) bladder, 397-401; toad, 398, 399, 401; urinary organs, 429, 437, 442, 443; urine, 436; urogenital ducts, 437, 466, 467, 468, 470, 474, 484; veins, 370-372; vertebrae, 525, 527, 528, 530, 531, 532
- Fisi*, 65
- Fisipectia*, 64, 65
- Flare*, 714; choroid, 808; dorsal, 680, 687, 688, 707; lateral cerebral, 714, 715; longitudinal cerebral, 708, 712; palpebral, 818; parieto-occipital, 714; portal, 317, 318; postcaval, 318; rhinal, 713; of Rolando, 714; of Sylvius, 713, 714, 715; umbilical, 317; ventral, 680, 681, 687, 688, 707, 713
- Fistula*, pharyngeal, 388; umbilical, 439
- Flagellum*, 200
- Flamingo*, 56
- Flatfish*, 397
- Flatworm*, 340, 428, 805
- Flavor*, 782
- Flexion*, 689
- Flexion*, 649
- Flexure of brain*, 705
- Flint*, 116, 117
- Flipper*, 631
- Flocculus*, 730
- Flounder*, 35, 231, 307
- Flow, menstrual*, 493
- Fluid, cerebro-spinal*, 377, 699; spermatic, 482; synovial, 321
- Fluke, of mammals*, 625
- Flycatcher*, 57, 246
- Flying, dragon*, 49, 201; fox, 63; lemur, 63, 201, 224; squirrel, 65, 67, 201
- Focusing*, 809, 816, 822
- Fold, genital*, 462; inner genital, 490; labio-scrotal, 490; metapleural, 22, 23; neural, 162, 163, 172, 173
- Follicle, Graafian*, 455, 493, 495, 509; hair, 221, 250, 254, 256, 761
- Follicular cell*, 159
- Folsom, points*, 128
- Fontanelle*, 596; frontal, 578, 596; mastoid, 578, 596; occipital, 578, 596; sphenoidal, 578, 596
- Food, capture*, 272; materials, 262, 265; pathway, 302, 303; prehension, 272, 273; storage, 197; synthesis, 600
- Foot*, 638, 639, 640; elephant, 239; glandular, 217, 218
- Foramen, acetabular*, 612, 613; caecum, 281, 282, 283, 500; endolymphatic, 558; epiphyseal, 558, 578, 586; glossopharyngeal, 558; ilio-sciatic, 614; interparietal, 586; interventricular, 705, 706, 708, 711, 712; ischiopubic, 612, 613; magnum, 558, 559, 566, 567, 570, 582, 591; of Monro, 704, 706, 712; obturator, 611, 612, 616; ophthalmic, 558; optic, 570; ovale, 356; of Panizza, 358, 359; perilymphatic, 558; pubic, 610, 611; spinal nerve, 523, 527, 538, 683; supracoracoid, 550; vagus, 558; of Winslow, 328
- Fore-brain*, 349
- Fornix*, 708, 714
- Fossa, endolymphatic*, 558; glenoid, 549, 550, 607, 608, 609, 619, 621, 622; mandibular, 596; temporal, 574, 579, 583, 584
- Fossils*, 96; human, 120
- FOSTER*, 767
- Fovea, centralis*, 807, 815; nasalis, 827; temporalis, 827
- Fowl*, 57, 238
- Fox*, 65, 222
- FRANCE, ANATOLE*, 702
- FRANKLIN*, 4
- Fregata*, 411
- Frenulum, labial*, 276, 278; lingual, 278
- Frequency*, 801
- Friction ridge*, 205, 237
- Frigidoreceptor*, 759, 766, 768
- Fritsch*, 715
- Frizzle*, 248
- Frog*, 38, 42; breathing mechanism of, 200; circulatory system, 334, 357, 378, 379; cricket, 43; development of, 169-173; digestive system, 266, 267, 271, 279, 282, 290; endocrine glands, 501, 503; integument, 201, 210, 218; kinds of, 43; reproduction, 431, 452, 456, 463, 471, 483; respiratory system, 403, 406, 407, 420, 421, 422; skeleton, 532, 576, 587, 611;

- spinal, 731; temperature effects, 765;
tree, 43, 217
- Frontal, 555, 561, 568, 569, 570, 574, 575,
578, 579, 580, 582, 589; plane, 8
- Frontoparietal, 581, 587
- FULTON, 419
- Fundulus, 624
- Funiculus, cuneatus, 707, 718; dorsal, 687,
688, 697; gracilis, 707, 718; lateral 687,
688; ventral, 687, 688
- Funnel, buccal, 22, 209; peritoneal, 444
- Fur, 253
- Furcula, 622
- Furrow, visceral, 387, 388
- Gadus*, 437, 453, 603
- Galea aponeurotica, 562, 663
- GALÉN, 380, 505
- Galeopithecus*, 63, 224
- Gall, bladder, 269, 305, 313, 316, 319, 320;
stomes, 316
- Galliformes, 57
- GALTON, 260
- GAMBITTA, 702
- Gamete, 156, 448, 464, 466, 472
- Gametogenesis, 463, 464
- Ganglion, 155, 676; autonomic, 675, 747;
cervical autonomic, 747, 748; chain, 680,
683, 745, 747, 748, 749, 750; ciliary, 733,
747; coeliac, 747, 750; collateral, 745,
747, 748, 749, 750; dorsal, 675, 680, 682,
683, 686, 694, 704, 745; Gasserian, 733,
741, 742; gastric, 511; geniculate, 734,
742; habenular, 704, 711, 724; jugular,
735; mesenteric, 747, 750; neural, 19,
20; nodosal, 735, 743; otic, 747; petrosal,
734, 743; spinal—see ganglion, dorsal;
spiral, 734, 797, 798, 800; stellate, 747,
748; submaxillary, 747; sympathetic, 680,
681, 735; terminal, 746, 750; vertebral—
See ganglion, chain; vestibular, 734, 742,
797
- Ganoid, 268, 312, 356, 462, 585; bony, 35;
cartilaginous, 34, 35, 532
- Ganoin, 230
- Garpik, 230, 462
- Gasterosteus*, 325, 453
- Gastralia, 551, 554, 615
- Gastric lipase, 311
- Gastrula, 160, 170
- Gastrulation, 161
- Gavial, 52
- Gecko, 49, 282, 404, 420
- Geese, 56
- GEGENBAUR, 604
- Genera, 14
- Gene, 181
- Genesis, 464
- Genetics, 181
- Genital, duct, 467, 468; eminence, 490; fold,
462; papilla, 462, 467; pore, 462; ridge,
455, 456, 460, 464, 489; tubercle, 489,
490
- Genitalia, external, 473-480, 489, 490
- Geologic time-scale, 103
- Geomys*, 294
- Geotaxis, 784
- Geotria*, 821
- Germ, cells, 157, 455, 458; layers, fate of,
167
- Germinal, cells, 685, 686; disc, 159
- Germ-line, 180
- Germplasm, 447, 449, 454, 455, 464
- Giantism, 185, 506
- Gibbon, 69, 125, 126
- Gila, monster, 51, 279
- Gill (branchia), 383, 387, 388, 391, 394;
of amniotes, 397; amphibian, 395, 396;
of amphioxus, 387-389; arches, 387, 394,
563, 572, 604; cyclostome, 390, 391;
dipnoan, 395; elasmobranch, 391, 394;
embryonic of dogfish, 393; external, 365,
395, 396; filaments, 368; ganoid, 393,
394; holoccephalan, 391, 394; internal,
365; invertebrate, 389; leaflike, 396;
opercular, 393; pinnate, 395; pouched,
390, 391; raker, 391, 392, 395; rays, 280;
sac, 391; septum, 388, 391, 392, 394; slits,
12, 362, 387, 388; teleost, 393, 394; tuni-
cate, 387, 388, 389
- Gingivae, 277
- Giraffa*, 74, 235
- Giraffe, 74, 274, 305, 404, 534
- Girardinus*, 475, 484
- Girdle, 540; pectoral, 521, 549, 550, 575,
608, 609, 618-622, 623; pelvic, 521, 532,
533, 605, 608, 609-618
- Gizzard, 306, 310
- Glaciation, 104
- Gladiolus, 552, 553
- Gland, 671; accessory sexual, 480; adrenal,
471, 499, 509; albumen, 485; alveolar,
215; ampullar, 481; anal, 270, 483; of
Bartholin, 482; Brunner's, 322, 327;
bulbo-urethral, 457, 482; byssal, 215;
carotid, 499, 510; cement, 215; ceru-
minous, 222; cervical, 481; choroid,
823; ciliary, 220, 818; cloacal, 483; coccy-
geal, 499; Cowper's, 476, 481, 482;
cranial, 504; ductless, 497; duodenal,
499; ear, 219, 222; von Ebner's, 285;
endocrine, 143, 497; excreting, 143;
exocrine, 143; femoral, 218, 473; gastric,
311, 327, 499; Harderian, 825, 828;
holocrine, 214; inguinal, 483; integu-
mentary, 208, 209, 210, 211, 212, 214-229,

- 315; intermaxillary, 279; of internal secretion, 497; interrenal, 511; labial, 275, 279; lacrimal, 222, 403, 819, 825, 828; Leydig's, 217; Lieberkühn's, 314, 322, 324, 327; light-producing, 216; lingual, 279; of Littre, 482; luminescent, 216; lymph, 337; mammary, 222, 223, 226, 228, 483; Meibomian, 221, 818, 819; merocrine, 214; milk, 222, 223, 226, 228, 483; molar, 275; of Moll, 220, 818; of mouth, 279; mucous, 200, 209, 210, 216, 279, 280, 327; multicellular, 211; necrobiotic—see gland, holocrine; nidamental, 485; odoriferous, 218; oral, 279; palatine, 278, 279; pancreatic, 499; parathyroid, 499, 500, 502; parotid, 276, 279, 734; perineal, 483; pharyngeal, 499, 504; pineal, 499, 507, 705, 707, 708, 710, 711, 724, 728, 729; pituitary—see hypophysis; poison, 210, 217, 279, 300; precuing, 218; preputial, 222; prostate, 457, 481, 482, 499; pterygopodial, 216; puberty, 459, 508; rectal, 270, 479; red, 398, 399; salivary, 276, 279, 280, 327; secret, 222, 483; sebaceous, 200, 205, 220-221, 221, 250, 254; secreting, 143; sexual, 483, 508; shell, 474; sublingual, 276, 278, 734; submaxillary, 276, 279, 483, 734; subpharyngeal, 26; suprarenal, 509, 510; sweat, 200, 201, 205, 219, 220, 257, 429; tarsal, 221, 818, 819; tear—see gland, lacrimal; thymus, 499-504; thyroid, 26, 281, 390, 499-502, 504; tubular, 215; types of, 214, 215; Tyson's, 481, 483; unicellular, 211; urethral, 482; uropygial, 218; uterine, 481, 483, 493; vestibular, 482; vitally-secretory—see gland, merocrine; vulval, 222; wax, 222, 791
- Glandulae epiploicae, 270, 325
- Glandular field, 281, 285
- Glans, clitoridis, 489; penis, 476, 477, 489, 490
- Glass snake, 50
- Glenoid fossa (cavity), 549, 550, 607, 608, 609, 619, 621, 622
- Globus, major, 469; minor, 469
- Glomerulus, 432, 433, 434, 435, 442, 443, 444, 455
- Glomus, 442
- Glottis, 304, 403, 421, 423
- Glycerol, 12, 333
- Glycogen, 205, 315
- Glycogenase, 323
- Glyptodon, 71, 233
- Gnath-, 27
- Gnathostomata, 29, 582
- Goat, 75, 222, 236, 252, 253, 334, 477; mountain, 127, 239
- Gobius, 787
- GODMAN, 80
- GOETHE, 6, 330, 595
- Goltre, 501
- GOLDSCHNEIDER, 766
- Golgi bodies, 130
- GOLL, 715
- Gonad, 165, 167, 178, 444, 454, 508
- Gooseflesh, 198, 251
- Gopher, 58, 276, 294
- Gorilla, 69, 125, 126, 544
- GOULD, 89
- Grampus, 79
- Granulocyte, 336
- Granulosum, 203, 204
- Gray matter, 686, 694, 695, 696
- Grebe, 56
- Grimaldi, 125
- Gristle, 145
- Groove, chiasmatic, 570; epibranchial, 390; epipharyngeal, 23, 24; lacrimal, 594; medullary—see groove, neural; nasolabial, 774, 775, 778; neural, 162, 176, 674; parovarian, 462; sperm, 476
- Grotto, painted, 111
- Ground bundle, 690, 693
- Grouse, 238
- Growth, 162
- Gruiformes, 57
- Gruiter, 400, 420
- Guanase, 323
- Guano, 99
- Gubernaculum testis, 459
- GUDERNACH, 503
- Guinea pig, 65, 285, 292, 316, 320, 445, 477, 513, 802
- Guitar fish, 31
- Gull, 57
- Gum, 277, 287
- Gustoreceptor, 759, 780
- Gut, postanal, 446
- Gymnarekus, 396
- Gymnophiona (Apoda), 38, 39, 40, 378, 407, 625
- Gymnoti, 400
- Gymnotus, 563
- Gynecomastium, 226, 227
- Gyrus, 714
- Habenula, 711
- Habenular, commissure, 707, 710, 711, 724; ganglion, 704, 711, 724; nucleus, 507
- Habit, 730
- Habitable earth, 108
- Habitat, 82
- Haddock, 307
- HAECKEL, 120, 702
- Haema-, 523

- Haemal, arch, 522, 523, 527, 528, 532;
 canal, 522, 523; spine, 475, 522, 523
 Haemoblast, 337
 Haemoglobin, 331, 333
 Haemolysis, 335
 Haemophilia, 340
 Haemopoiesis, 335, 348
 HAEMFEL, 332
 Haemulonidae, 400, 401
 Hagfish, 25, 455, 463, 532
 Hair, 201, 205, 221, 249-257; angora, 256;
 bulb of, 250, 254; color of, 256; cortex
 of, 250; curly, 255; currents, 251; cuticle
 of, 250; definitive, 256; development,
 254; follicle, 221, 250, 254, 256, 761; fur,
 253; germ, 254; gray, 256; groups, 253;
 guard, 253; kinky, 255; medulla of,
 250; papilla of, 221, 250, 254; pigment
 of, 256; shaft, 221, 254; sheath, 221, 250,
 254; sinus, 253; straight, 255; wavy,
 255
 Hake, 293
 Halicore, 78, 299
 Halmaturus, 61
 Hamatum, 629, 632
 Hammer, 582
 Hamster, 307, 481
 Hand, 626, 640
 Hapale, 679
 Hare, 65, 256, 285
 Harelip, 775
 Harrimania, 18
 HARRISON, 179
 HARVEY, 341
 HASWELL, 30
 Haustrea, 270, 325
 Haversian canal, 148, 149, 152
 Hawk, 56, 238, 461
 HAWTHORNE, 789
 Head, 6; of rib, 543, 546
 Headfish, 397
 Hearing, 716, 717, 788, 800
 Heart, 341, 348, 350, 351, 351-363; ath-
 lete's, 186; atrium, 354, 355; auricle,
 355, 356, 359, 361, 363; autonomic in-
 nervation, 751; conus, 354-357, 363; de-
 velopment of, 352, 353; evolution of, 355;
 human, 358; lymph, 378, 379; position
 of, 359, 360; sinus, 354-357, 363; size of,
 359; valves of, 361; ventral, 11; ven-
 tricle, 354-358, 359, 361, 363; work of,
 361
 Heat, 692
 HECHT, 814
 Hedgehog, European, 63, 213, 233, 252,
 481, 660
 Heel, 639
 HEGNER, 20, 26, 51, 126
 Heidelberg man, 122-123, 124, 125, 126
 Helicotrema, 797, 798, 799
 Helix, 789
 Hellbender, 41
 HELMHOLTZ, 754
 Heloderma, 51, 279
 Hemichordata, 17-18
 Hemi-embryo, 179
 Hemipenis, 475
 Hemispheres, cerebellar, 708, 709, 710;
 cerebral, 712, 714, 716, 717, 725, 726
 Hen, 306, 334, 471, 473, 485, 493, 509
 HENNING, 774
 HENKION, 97
 Hepat-, 11
 Hepatic portal, 11, 24, 317, 342, 343, 360,
 371, 373, 375, 376
Heptanchus, 392, 565
 Herbivore, 264, 273, 274, 280, 296, 297,
 313, 318
 Hereditary handicap, 186
 Hermaphroditism, 463, 491
 Hernia, 460
 HERODOTUS, 110
 Heron, 56, 245
 HERRICK, 716
 Herring, 35, 307, 463
Hesperornis, 55, 291
 HESSE, 782
 Heterocercal, 623, 624
 Heterocoelous, 529, 530
Heterodon, 51
 Heterodont, 294, 295, 297
Heterotis, 396
Hexanchus, 364, 392, 453
 Hibernation, 33, 37
 Hill, milk, 225, 226
 Hilus, 431, 434
 Hind-brain, 349
 Hip, 628
Hipparion, 99
Hippidium, 99
Hippocampus, 28, 232, 485, 545
 HIPPOCRATES, 301, 380, 597
Hippopotamus, 73, 97, 121, 220, 249, 274,
 425
 Histology, 141, 270
 HIRSH, 715
 Hoatzin, 238, 306
 Hog, 73
 HOLBEIN, 646
 Holdfasts, 472
 HOLMES, 219
 Holobranch, 388, 391
 Holocephali, 29, 31-32, 393, 545, 564
 Holos, 32, 35
 Holstei, 34, 35, 393
 Hominidae, 70

- Homo, diluvii testis*, 120; *heidelbergensis*, 122, 123, 126; *neanderthalensis*, 125, 126; *sapiens*, 70, 125, 126
 Homocercal, 623, 624
 Homodont, 294, 295
 Homology, 607
 Homology, urogenital, 487
 Honey bee, 385, 679
 Hoof, 237, 239
 Hook, anal, 473; of clasper, 474; feather, 243, 244
 Hooke, 129
 Hooton, 127, 294
 Hormone, 143, 254, 320, 331, 339, 456, 497-513; gonadotropic, 506; growth, 506; thyrotropic, 506
 Horn, 233-236, 508; dorsal, 686, 687, 690, 697, 720; hollow, 236; keratin-fiber, 234; ventral, 686, 687, 690, 697
 Horned toad, 50, 51, 293, 234, 374
 Horse, 73, 334, 420, 480, 603; digestive system, 285, 294, 297, 305, 316; integument, 220, 222, 223, 225, 239, 242, 252; pedigree of, 99; wild, 112, 127, 250
 HOSKINS, 503
 HOWELL, 339, 419
 HUBER, 687, 696, 697, 821
 HUETTNER, 130, 135, 161, 163, 169, 170
 Humerus, 607, 627, 628, 631, 632
 Hummingbird, 57
 Humor, aqueous, 816
 Hunger, 262, 831
 HUTCHINSON, 315
 HUXLEY, 101, 128, 261
 Hyacens, 64, 65, 125, 295, 480
 Hydra, 265, 602
 Hyla, 38, 42, 43, 422, 473
 Hylabates, 69, 308
 Hylodes, 386
 Hymen, 479, 480, 487
 Hyobranchial apparatus, 283, 284, 571, 572, 576
 Hyoid, 281, 283, 424, 425, 565, 571, 572, 577, 578
 Hyomandibular, 563, 564, 565, 571, 573, 575, 580, 582
 Hyostylic, 564
 Hypaxial, 178
 Hypermastism, 226, 227
 Hyperoödon, 79, 547
 Hyperthelium, 226, 227
 Hypertrichosis, 257
 Hypertrophy, 185
 Hypobranchial, 280, 563, 576
 Hypocentrum, 528, 529, 534
 Hypodermis, 200, 207
 Hypohippus, 99
 Hypohyal, 576
 Hypomere, 164, 167, 168
 Hyponychium, 240
 Hypophysis, 499, 504, 505, 704, 705, 708, 710, 711, 723, 724, 725, 726, 728
 Hypospadias, 491
 Hypostomus, 386
 Hypothalamus, 711
 Hypothecar, 258
 Hypsodont, 296
 Hyracoides, 62, 77, 412
 Hyrax, 313, 439
 Ice Ages, 104, 127
 Ichthyo-, 29
 Ichthyomyzon, 27
 Ichthyophis, 38, 40, 212
 Ichthyornis, 55, 291
 Ichthyosaur, 46, 47, 531, 625
 Iguana, 50, 550
 Iguanodon, 46
 Ileum, 305, 313, 314
 Ilium, 532, 607, 608, 609, 610, 611-616, 628
 Impulse, 155, 665
 Incisor, 294, 295
 Incubation, 452
 Incubatorium, 227
 Incus, 565, 571, 572, 580, 582, 791-793, 798
 Indirect path, 4
 Individual, 14
 Inferior, 9
 Inflammation, 337
 Infundibulum, 505, 704, 705, 708, 711, 712, 723, 724, 726, 728
 Inguinal canal, 459
 Inhibitor, 731
 Innominate bone, 615, 628
 Inscriptions tendineae, 656
 Insect, 5, 200, 201, 216, 385, 420, 472, 498
 Insectivora, 62, 67, 92, 220, 223, 285, 298, 313, 376, 431, 480, 714
 Insertion of muscle, 647
 Inspiration, 415, 418, 419
 Instep, 629
 Instinct, 494, 730
 Insula, 512
 Inaulin, 312
 Intake, 262
 Integument, amphibian, 196, 210, 211, 212, 217; amphioxus, 208; area of, 202; bird, 201, 213, 218, 242; color of, 202; cyclostome, 209; embryonic, 206; fish, 196, 211, 216, 217, 229-232, 241; friction, 205, 257; human, 201-207, 208, 219-228; invertebrate, 200, 207, 215, 216; mammalian, 213, 219-228; molt-

- ing of—see ecdysis; pigment, 204, 205, 210; reptilian, 212, 213, 218, 232; respiratory, 37; shedding of, 197; thickest, 202; thinnest, 201; tunicate, 208; uses of, 196-201
 Interbasal, 526
 Intercalary, 527
 Interclavicle, 550, 551, 619, 620-622
 Interdigital tori, 258
 Interdorsal, 521, 526, 527, 528, 529, 532, 535
 Intermaxillary, 595
 Intermedium, 627, 628
 Interoceptor, 758, 759, 831
 Interopercular, 564, 575
 Interparietal, 568, 574, 581
 Interphase, 135
 Interrenal, 511
 Interventral, 521, 526, 527, 529
 Intestinal portal, anterior, 349
 Intestine, 164, 269, 271; large, 269, 270, 311, 324-326; small, 305, 306, 311-314
 Invagination, 10, 161, 674, 705
 Inverteae, 323
 Investing bone, 150
 Iodine, 501
 Iodopsin, 814
 Iris, 807, 809, 810, 817, 818, 828
 Irritability, 756
 Irritoreceptor, 759, 783
 Ischiopubis, 609, 610
 Ischium, 532, 548, 607, 608, 609, 613, 611-616, 628
 Islands, blood, 348, 349, 350; of Langerhans, 320, 321, 512
 Iso-, 158
 Isolecithal, 158
 Isopodin, 230
 Isotropic bands, 154
 Isthmus, of fauces, 304; of thyroid, 500
 Ivory, 288

 Jacana, 238, 242
 JACONI, 492
 Java man, 120-122, 125, 126
 Jaw, 148, 563; gorilla, 599; Heidelberg, 123, 599; human, 148, 295, 599; parrot, 590; snake, 588; Spy man, 599; suspension of, 564, 565; upper movable, 588, 590
 Jejunum, 313, 314
 Jellyfish, 785
 Jerboa, 67
 Joint, 520; ball and socket, 520, 530, 631; hinge, 520, 631; mesotarsal, 635; saddle, 530
 JORDAN, 14, 401, 531
 Jugal, 568, 574, 578, 579, 581, 589
 Jumbo, 76
 Jurassic, 103

 KAMMERER, 473
 Kangaroo, 60, 61, 220, 297, 419, 476, 677
 KAPPERS, 687, 695, 696, 821
 KATZ, 763
 Keel, sternal, 519, 551
 KEEN, 128, 140, 189, 256, 362, 352
 KEITH, 124, 363, 489, 684, 717
 KENDALL, 501
 KEPNER, 146
 Keratin, 234
 Kerato-hyalin, 204
 Kidney, 165, 178, 200, 428, 429-436, 430, 431, 437, 471, 481; compensating, 430; horseshoe, 430; human, 431; lobulated, 429, 430, 432; sexual, 469; shapes of, 429; unipyrarnidal, 431, 432; urinary, 469
 Kingdom, 14
 Kingfisher, 57
 Kinglet, 57
 KINGSLEY, 779
 Kitchen midden, 110
 Kiwi—see *Apteryx*
 KLAATSCH, 120
 Knee-cap, 649
 Knee-jerk, 671
 Knee-pads, 242
 Koala, 60, 61
 VON KOENIGSWALD, 121
 KROGH, 346

 Labia, majora, 479, 480, 489, 490; minora, 479, 480, 489, 490
 Labial cartilage, 280, 565
Labidosaurus, 45, 621
 Labyrinth, bony, 795; membranous, 786, 795, 796; respiratory, 386
 Labyrinthodont, 39-40
Lacerta, 218, 445, 576, 778
 Lacertilia, 49
 Lacrimal, 561, 568, 574, 578, 579, 581, 589
 Lact-, 324
 Lactase, 323
 Lactation, 494, 509
 Lactal, 314, 324, 343, 378
 Lactic-acid ferment, 323
 Lacunar, 149
 Lagna, 791, 802-804
 LAMARCK, 202
 Lamellae, of bone, 147, 148, 149; circumferential, 148, 149; concentric, 148, 149; interstitial, 148, 149
 Lamina, dental, 288, 289; spiral, 797, 798; terminal, 705, 706, 708, 712, 713, 725

- Lamna*, 392
Lampetra, 27
Lamprey eel, 25, 26, 209, 267, 318, 319, 333, 334, 455, 463, 525, 532, 536
Lamprolatus, 51
Lancelet, 22
Langley, 744, 746
Lanugo, 355
Laryngo-pharynx, 303, 304
Larynx, 304, 420, 421-425, 571, 572, 577, 735
Latebra, 452
Lateral-line canal, 769, 770
Latimeria, 32
Latin, 16
Lavoisier, 383
Law, of distribution, 83; of overpopulation, 85; paleontological, 104; of priority, 16
Layer, choroid, 807, 809, 810; corneal, 203, 204, 205; cependymal, 685, 686; germ, 167; meninx, 203, 204; lucidum, 203, 204, 240; Malpighian, 203, 204, 205; mantle, 685, 686; marginal, 685, 686; nervous of retina, 808, 814; papillary, 205, 206; pigment of retina, 808, 814; reticular, 206; retinal, 808; sclerotic, 11, 509, 807, 809, 817; subcutaneous, 523, 205, 206
Learning, 220
Leather, 204
Leatherback, 48
Lecithin, 158
Van Leeuwenhoek, 333, 341
Left-handedness, 646
Leg, embryonic, 11
Leisy, 99
Lemniscus, median, 718, 719, 720
Lemur, 67, 68, 233, 241, 298, 420, 478, 480, 679; flying, 63, 201, 224
Lemuroidea, 68
Leis, 807, 808, 809, 810, 816, 817, 818
Lepidotriton, 33, 395, 406
Lepidosteus, 35, 230, 437, 438, 462, 530
Leptobas, 121
Leptocephalus, 770
Lepus, 65, 256, 439
Leucocytes, 132, 335-338, 336
Lewis, 131, 257, 469
Leydig, 761
Life, realms, 91; whirlpool of, 261
Ligament, broad, 479, 487; falciform, 318, 328; round, 317, 319; sacro-iliac, 617; spiral, 797, 798; suspensory, 810, 816, 817; transverse of atlas, 534; ventral of bladder, 328, 439; ventral of liver, 328; vesico-umbilical, 438
Ligamentum carpi, 631
Light, 21
Light ration, 491
Line, milk, 224, 225, 226
Linnaeus, 16, 26, 27
Linne, 16
Lion, 65, 295, 420
Lip, 274, 278
Lipase, 311, 323, 327
Lister, 188
Liver, 11, 24, 167, 172, 305, 306, 315-319, 318, 319, 327; development of, 319
Living, rate of, 261
Lizard, 43, 49-50, 438; digestive system, 279, 282, 293, 300, 307; endocrine glands, 507; Jacobson's organ, 778; legless, 625; nose-horn, 234; reproductive system, 461, 463, 473, 475; skeleton, 539, 554, 576, 625; trachea, 403; veins, 374
Llama, 74, 334
Lobe, caudate, 318, 319; electric, 723, 727; frontal, 714; inferior of brain, 726; occipital, 714, 740; olfactory, 701, 704, 712, 724, 725, 727-729, 733; optic, 704, 723-726, 727-729, 739, 740; parietal, 714; pituitary, anterior, 505, 506; pituitary, intermediate, 506; pituitary, posterior, 505, 711; pulmonary, 412; pyriform, 712, 713; quadrate, 318, 319; temporal, 714, 743; trigeminal, 723; vagus, 723
Lobule, ear, 789; renal, 435
Localization, cerebral, 715-718
Locomotion, 29, 201, 319, 600, 604, 630, 642
Loggerhead, 48
Logos, 82
Lonchocera, 253
Loon, 56
Loop, aortic (arterial), 348, 350, 351, 354-368; Henle's, 433, 434, 435; radial, 259; ulnar, 259
Lophodont, 296
Loudness, 801
Loxodonta, 76
Lurodon, 463
Lucidum, 203, 204, 240
Lull, 97
Lunatum, 628, 632
Lung, 318, 385, 401-414; atrium, 408; capacity, 419; development of, 413; phylogeny of, 406
Lungfish, 400, 492
Lunula, 240
Lutein, 465, 509
Lutra, 64, 253
Lutz, 88
Lyell, 96, 97
Lymph, 142, 377; node, 337, 380; sac, 379

- Lymphatic, 204, 343, 344, 346, 377-381, 378
 Lymphocyte, 336
 Lynx, 64
 Lyre birds, 248
- Macacus*, 69, 285, 679, 789
 MACFIE, 429
 Mackerel, 35, 268, 312, 463, 624
Macrochelys, 49
Macropodus, 386
Macropus, 60, 220
 Macrosmatic, 774
Macula, communis, 802; *lagenae*, 786, 802, 803; *lutea*, 815; *neglecta*, 802, 803; *sacculi*, 786, 796, 797, 803; *utriculi*, 786, 796, 797, 803
 Magdalenian, 118, 119
 MAGENDIE, 684
 Magnum, 629
Malapterurus, 663
 Malar, 295, 555, 595
 Malaria, 188
 Mallard, 422
 Malleus, 565, 570, 571, 572, 573, 581, 582, 791-793
 МАЛПЕТ, 3
 МАЛПЮИ, 203, 341
 Maltase, 323, 327
 MALTHUS, 85
 Mammæ, 57, 222, 223; supernumerary, 226, 227
 Mammal, adrenal glands, 509, 510; age of, 103; aortic loops, 367, 368; appendages, 603, 625, 630, 631, 635-641; archipallium, 712; blood platelets, 338; brain, 706-716, 725, 729; breathing, 418; breeding, 491-494; bronchioles, 405; circulation plan, 343; claw, 237, 238, 239; clitoris, 480; colic caeca, 269; copulation, 473; development of, 173, 174, 175; digestive system, 270, 272; egg, 158, 453, 454; epidermal glands, 219-228; erythrocytes, 333; fetal envelopes, 486; fin, 625; friction ridges, 257-260; hair, 249-257; hard palate, 302; heart, 355, 361; integument, 213, 214, 219-228; intestine, 313, 324; islands of Langerhans, 512; kidney, 431, 445; larynx, 423-425; lungs, 412; lymph hearts, 379; meninges, 699, 700; mesonephros, 445; metanephros, 445; mouth glands, 279; muscles, 655, 656, 660-663; nerve cord, 687, 688-695, 698; occipital condyles, 568, 591, 592; ovary, 461, 463, 509; pancreas, 321; parathyroid glands, 502; pectoral girdle, 621, 622, 623; pelvic girdle, 615-618; penis, 476, 477, 478; pineal body (epiphysis), 507; pituitary gland, 504, 505, 506; prostate gland, 482; ribs, 547; scales, 213, 233; seminal vesicle, 491; sense organs, 774, 777, 779, 781, 788-804, 806-820, 828-830; skull, 555, 562, 566-582, 568, 570, 578, 582, 590-600, 598; sternum, 551, 552; stomach, 308; teeth, 291-293, 295; testes, 457, 508; thymus gland, 501, 503, 504; thyroid gland, 500; tongue, 282, 283-287; trachea, 404; urinary bladder, 438, 439; urine, 436; urogenital ducts, 468, 469, 470; vagina, 479; veins, 375, 376; vertebrae, 525, 528, 531, 534; voice, 420
 Mammalia, 17, 57-80
 Mammary, apparatus, development of, 224, 225, 226; body, 708, 710, 711, 712, 713
 Mammoth, 76, 96, 100, 112, 124, 299
 Manatee, 78
 Mandible, 555, 582, 775
 Mandibular arch, 281, 562, 573, 577
 Mandrill, 243
 Mane, 250
Manis, 71, 221, 233, 291
 Mantle, 268
 Manubrium, 551, 552, 553, 622
 Marmoset, 679
 Marrow, 148, 151, 152
 Marsh bird, 57
 Marsipobranch, 390
 MARSTON, 124
 Marsupial, bone, 617; digestive system, 285, 291, 292, 313; kidney, 431; larynx, 425; nipple, 225; pouch, 227; reproductive system, 470, 478, 481, 492; veins, 376
 Marsupialia, 59, 60, 61, 92
 Marsupium, 59, 227, 485
 Marten, 295, 481
 Mass, inner cell, 174
 Massa intermedia, 708
 Mastication, 274, 309
 Mastoid cells, 596, 791
 Matter, gray, 686, 694, 695, 696; white, 686, 695
 Maturation, 136-138, 136, 464
 MAVOA, 271
 Maxilla, 555, 578, 582, 775
 Maxillary, 568, 574, 575, 578, 579, 581, 587, 588, 589
 Meatus (canal), auditory, external, 397, 788-791, 792
 Meckel's cartilage, 280
 Mediastinum, 402
 Medicine, creative, 191; curative, 191; preventive, 191
 Medulla, of adrenals, 510, 511; of hair, 250; oblongata, 693, 706, 707, 788, 709,

- 710, 720, 721-727; of ovary, 463; renal, 431, 435
- Medusae, 340
- Megalith, 113
- Megaptera, 79
- Meiosis, 136-138
- Membrane, hasilar, 798, 802; branchiostegal, 415; cell, 130; embryonic, 37, 43, 44, 166, 318, 351, 386, 486; mucous, 195, 275, 280, 479; nictitating, 741, 818, 825; nuclear, 129; olfactory, 776; periodontal 287; Reissner's, 798; Schneiderian, 403; semilunar, 423; shell, 452; synovial, 520; tectorial, 798, 799, 800; thyrohyoid, 425; tympanic, 573, 579, 596, 791, 792, 793, 794; tympaniform internal, 423; vestibular, 798; vitelline, 159, 452
- Mendelism, 181
- Menhir, 113
- Meninx, 538, 698, 699; primitiva, 699
- Menopause, 493
- Menstruation, 481, 493, 508
- MENTEL, 646
- Mercator map, 93
- Merlucius, 269
- Mermaid, 77
- Merychippus, 99
- Mesencephalon, 349, 703, 704, 710
- Mesenchymæ, 165, 167, 168
- Mesentery, 326; dorsal, 165, 167, 172, 178, 326; proper, 328; ventral, 163, 167, 326
- Mesethmoid, 561, 568, 569, 580
- Mesobronchus, 409
- Mesocardium, 352, 353, 354
- Mesocoele, 705, 706
- Mesocolon, 328
- Mesocuneiform, 629
- Mesodæum, 270
- Mesoderm, 163, 167, 168, 171, 173, 174, 175, 176, 206; differentiation of, 164, 172; formation of, 164; somatic, 162, 164, 172; splanchnic, 162, 164, 172
- Mesogaster, 328, 430
- Meshippus, 99
- Mesolithic, 118, 119
- Mesomere, 164, 165, 167, 168
- Mesonephridia, 443, 444, 467, 468, 469, 470
- Mesonephros, 267, 440, 443, 444, 445, 456, 462, 467, 468, 471, 474, 487, 511
- Mesopterygium, 619
- Mesorchium, 456, 474
- Mesorectum, 328
- Mesotubarium, 474
- Mesovarium, 460, 474, 479
- Mesozoic, 45, 103, 127
- MESSER, 675
- Meta, 59
- Metabolism, 5; calcium, 503; carbohydrate, 512
- Metacarpal, 607, 627, 629, 632
- Metacoelæ, 705
- Metacónid, 298
- Metacónus, 298
- Metamere, 9
- Metamerism, 9
- Metamorphosis, amphibian, 37, 268; tunicate, 19, 20; urodele, 41
- Metanephridia, 445
- Metanephros, 440, 445, 461, 468
- Metaphase, 134, 135
- Metapleural fold, 22, 23
- Metapterygium, 609, 619
- Metapterygoid, 575
- Metatarsal, 607, 627, 629, 638
- Metatheria, 58-60, 59
- METCHNIKOF, 325
- Metencephalon, 703, 704, 709
- MEYER, 617
- MICHELANGELO, 646
- Microcebus, 68
- Microconodon, 298
- Micron, 334
- Micropathology, 189
- Microsmatic, 774
- Micurus, 51
- Micturition, 439
- Midas, 253
- Midbrain, 349, 710
- Milk, 223; bird's, 304, 306; canal, 226; field, 225, 226; gland, 222, 223, 226, 228, 483; hill, 223, 226; line, 224, 225, 226; pigeon's, 306; pocket, 225, 226; production, 509; uterine, 483
- Mink, 65
- Minor, 700
- Miocene, 125
- MIRABEAU, 292
- Mirgurus, 386
- Mistichthys, 27
- Mistletoe, 87
- MITCHELL, 436, 830
- Mitosis, 133-135, 135
- Moa, 56, 96, 622
- Modiolus, 797
- Mola, 397
- Molar, 294; teeth, 298
- Mole, 58, 62, 63; cervical vertebrae, 535; digestive system, 285, 292, 298; integument, 221, 233, 251; marsupial, 61; reproductive system, 478, 480, 481
- Molgula, 18
- Mollusk, 12, 196, 273
- Molting, 247, 249, 257
- Mongoose, 295

- Monkey, 58, 67, 68, 69, 257, 276, 313, 419, 420, 425, 478, 480, 679
 Mono-, 58
 Monocytes, 336
 Monodon, 79, 299
 Monoestrous, 493
 Monophyodont, 292
 Monotremata, 58, 59, 92
 Monotreme, cerebrum, 714; digestive system, 276, 285, 291, 300, 313, 325; integument, 227, 242; reproductive system, 478, 481; respiratory system, 412, 423; urinary bladder, 438
 Mons Veneris, 480, 491
 Monuments, 113
 Moore, 460
 Moose, 75, 235
 Mormyrus, 461
 Morphology, 6, 13, 182
 Moxa, 414
 Moth, 772
 Mounds, 114
 Mouse, 65, 220, 223, 233, 256, 297, 308, 420, 445, 481; spiny, 252; waltzing, 787
 Moustertian, 117, 118
 Mouth, 6, 274; of alligator, 274; of nestling bird, 274; protrusible, 273; roof of, 277, 302
 Movement, hinge, 520, 631; of tongue, 281-284; of vertebrae, 538
 Mucosa, 270, 271, 479
 Mucus, 196
 Mud puppy, 40, 41, 202, 407
 Müller, 313, 754
 Multiangulum, majus, 629, 632; minor, 629, 632
 Muraena, 777
 Mus, 65
 Muscle, 642; abductor, 658; acromiodeltoid, 655; acromiotrapezius, 655; action, 152; adductor, 658; antagonistic, 152, 643; appendicular, 651, 657; arrector pili, 221, 251; aryteno-epiglottic, 425; axial, 651, 652; biceps brachii, 646, 647; biceps femoris, 655; brachialis, 650, 655; branchiomeris, 167, 651, 658, 742; buccinator, 663; cardiac, 154; cat, 650, 655; caudofemoralis, 655; cephalohumeral, 655; cheek, 662, 663; ciliary, 740, 807, 810, 817, 818; circular, 271; clavo-brachialis, 650; colli, 655; crico-thyroid, 425; deltoid, 647; depressor, 658; digastric, 653, 654, 655, 659, 734; dilator pupillae, 811, 817; dorsal trunk, 656; dorsalis scapulae, 654; drumming, 401; ear, 662, 663, 790; ectotriceps, 650, 655; elevator, 658; endotriceps, 650; epaxial, 178, 654; epitrochlear, 650; external intercostal, 653; external oblique, 654, 655; external rectus, 653, 726, 734, 741; extrinsic, 281, 283; eyeball extrinsic, 652, 653, 817; eyebrow, 662; facial, 661, 734, 742; fin, 658; gastrocnemius, 655; genioglossal, 281, 653; geniohyoid, 653, 654, 655; gluteus maximus, 655; head, 652; heart, 154; homologous, 647; human, 648, 663; hyoglossal, 281, 653, 654; hypaxial, 178, 654; inferior oblique, 652, 653, 733, 740; inferior rectus, 652, 653, 733, 740; insertion of, 647; integumental, 651, 659; internal intercostal, 655; internal oblique, 654; internal rectus, 652, 653, 726, 733, 740; intestinal, 271; intrinsic, 281; involuntary, 154, 167, 651; iris, 651, 740, 811, 817; latissimus dorsi, 654, 655; leg, 650; levator palpebrae, 662, 740, 818; levatores arcuum, 654; lingualis, 654; lip, 662, 663; longissimus dorsi, 656; longitudinal, 271; masseter, 654, 655, 659; meditriceps, 650, 655; metameric, 651, 652; mimetic, 661; mylohyoid, 653; nasal, 662; obturator internus, 655; orbicularis oculi, 662, 663, 818; panniculus carnosus, 661; papillary, 361; patagial, 660; pectoantibrachialis, 650; pectoral, 223, 647, 650, 655; platysma, 662, 734; procoracohumeralis, 654; progressive, 663; psoas, 655; rectus abdominis, 654, 656; regressive, 663; retractor bulbi, 653, 741; salamander, 654; sartorius, 655; scalenus, 655; scalp, 734; semitendinosus, 655; serratus, 647, 655; shuddering, 661; smooth, 153; sonificus, 401; sphincter, 656; sphincter colli, 661, 662; sphincter pupillae, 811, 817; spinodeltoid, 655; spinotraperius, 655; stapedius, 659, 794; sternalis, 662; sternocleidomastoid, 659, 735, 744; sternohyoid, 655; sternomastoid, 655; sternothyroid, 655; striated, 153, 154; styloglossal, 653, 654; stylohyoid, 653, 655, 659, 734; superior oblique, 652, 653, 726, 733, 741; superior rectus, 652, 653, 726, 733, 740; temporal, 655, 659; tensor fasciae latae, 655; tensor tympani, 659, 794; thyroarytenoid, 425; thyrohyoid, 425, 655; tongue, 653, 735; transversus, 654; trapezius, 647, 654, 659, 735, 744; ventral trunk, 654; voluntary, 154, 167; xiphohumeralis, 655
 Muscular-sense, proprioceptive, 692, 717, 719, 785, 830
 Musculus, 647
 Musk, 773; deer, 222, 334; ox, 75
 Muskrat, 65, 67
 Mussel, 215

- Myctodera, 396
 Myelencephalon, 703, 704
 Myelination, 689, 697
 Myelocoele, 705
 Myliobatidae, 460
 Myo-, 165
 Myocardium, 352, 353
 Myocommata, 22, 522, 650
 Myofibrils, 152, 153, 643
 Myology, 643
Myopotamus, 253
 Myoseptum, 521
Myotis, 65
 Myotome, 22, 165, 526, 647, 650, 651
Myrmecophaga, 70, 291, 313
Mystacoceti, 79, 291
 Myxedema, 501
Myxine, 26, 27, 391, 463, 505, 723, 787
Myzon, 26

 Nails, 237, 239, 240, 241
 Name, scientific, 15
 NAPOLEON, 646
 Naris, external (anterior), 302, 574, 578, 579, 587, 591, 775, 778; internal, 302, 587, 778
 Narwhal, 79, 299
 Nasal, bone, 555, 561, 568, 574, 578, 579, 581, 582, 587, 589; capsule, 280, 565; cartilage, 594; cavity, 303, 401, 403, 412; muscles, 662; septum, 570; valves, 416;
 Nasopharynx, 303, 403
 Naso-turbinal, 568
 Navicular, 628, 629, 632, 638
 NEAL, 175, 613, 653
 Neanderthal, 122, 124, 125, 126, 127
 Neck, 533; of rib, 543; of tooth, 287
Neoturus, 41, 202, 293, 378, 396, 406, 408, 416, 421, 530, 548, 549, 569, 576
 Nematocyst, 215
 Neo-, 54
Neoceratodus, 33, 395, 406, 471, 627
 Neolith, 117
 Neolithic, 116, 117, 118, 119
 Neomorph, 524
 Neopallium, 712, 728
 Neornithes, 54, 55-57
 Neosternum, 551, 554
 Nephridia, 428, 432, 440
 Nephridiopore, 440
 Nephrocoele, 441, 442
 Nephrostome, 440, 441, 442, 443, 444, 446, 455, 470
 Nephrotome, 441
Nereis, 9
 Nerve, 155, 676; abducens (VI), 653, 708, 713, 726, 734, 736, 737, 740, 741; acoustic (auditory) (VIII), 708, 713, 726, 734, 736, 737, 742, 797; branchial, 743; cervical, 680, 708; chain, sympathetic, 681; cochlear, 742, 797; cord, 12, 20, 144, 164, 178, 267, 442, 522, 677-698; cranial, 677, 708, 713, 726, 731-744; cranial, mixed, 736; cranial, motor, 736; cranial, sensory, 736; endings, 204, 757; facial (VII), 659, 708, 713, 734, 736, 737, 742, 770, 780, 781; fiber, 666; glossopharyngeal (IX), 659, 708, 713, 726, 734, 736, 737, 743, 770, 781; hyomandibular, 726, 742; hypoglossus (XII), 650, 708, 713, 735, 736, 737, 744; infraorbital trunk, 726; lateral, 726, 743; mandibular, 726, 737; maxillary, 741; oculomotor (III), 652, 653, 708, 710, 713, 726, 733, 736, 737, 740; olfactory (I), 712, 733, 736-738; ophthalmic, deep, 726, 741; ophthalmic, superficial, 726, 741; optic (II), 653, 708, 713, 725, 726, 733, 736-738, 739, 807, 809; palatine, 726, 742; pelvic, 747; pharyngeal, 726; phrenic, 648, 657; postrematic, 726; pretrematic, 726; spinal, 527, 677, 679-685; spinal accessory (XI), 659, 708, 713, 733, 736, 737, 744; spino-cranial, 732; spino-occipital, 736; splanchnic, 747; terminal (O), 726, 733, 736, 737; trigeminal (V), 659, 708, 713, 733, 736, 737, 741, 771; trochlear (IV), 652, 653, 705, 708, 726, 733, 736, 737, 740, 741; vagus (X), 541, 659, 708, 713, 726, 733, 736, 737, 743, 770, 781; vaso-dilator, 477; vaso-motor, 348; vestibular, 742, 797; visceral, 726, 743
 Nervous, pathways, autonomic, 747; pathways, cranio-spinal, 718-722; system, autonomic, 676, 744-752, 747; system, central, 676; system, parasympathetic, 747, 751; system, peripheral, 676; system, sympathetic, 510, 747, 751
 Network, nerve, 673
 Neutral, arch, 522, 525, 527, 528, 533; canal, 522; crests, 674, 675; folds, 162, 163, 172, 173; ganglion, 19, 20; groove, 162, 176, 674; plate, 161, 162, 172, 173, 527, 533, 674, 675; spine, 521-523, 525; tube, 163, 172, 349, 522, 674, 675
 Neurenteric canal, 163, 164
 Neurite, 155, 668, 667
 Neuroblast, 667, 685, 686
 Neurocoele, 163
 Neurocranium, 280, 555, 558, 559
 Neurofibril, 155, 669
 Neuroglia, 155, 666, 685, 686, 812
 Neurohumor, 217, 667
 Neurohypophysis, 504

- Neurolemma, 668, 669
 Neuromast, 769, 770
 Neuron, 155, 666, 685; afferent, 687; association, 671, 694; bipolar, 668; efferent, 687; ganglionic, of retina, 811, 812, 814; intermediate, 671, 718-721, 745; intermediate, of retina, 811, 812, 814; motor, 673, 687, 694; multipolar, 668, 669; post-ganglionic, 745-749; preganglionic, 745-749; receptor, of retina, 811, 812; relaying, 671, 694, 718-721; of second order, 718-721; sensory, 673, 687, 690, 694, 695, 701, 776; somatic afferent, 732; somatic efferent, 732; somatic motor, 687, 745; somatic sensory, 687, 745; unipolar, 668; visceral afferent (sensory), 687, 732, 745; visceral efferent (motor), 687, 732, 746
 Neuropore, 163, 349, 674
 Neutrophil, 336
 NEWMAN, 32, 40, 41, 42, 44, 45, 47, 48, 49, 55, 61, 62, 64, 65, 68, 217, 441
 Newton, 40, 536
 Nipple, 222, 223, 224, 225, 226, 227
 Nociceptor, 768, 830
 Node, auriculo-ventricular, 363; Hensen's, 349; lymph, 337, 380; of Ranvier, 669; sinu-auricular, 363
 Non-adaptability, 89
 Non-chordate, 12
 Nose, brain, 703
 Nostrils—see nares
 Notochord, 9, 12, 144, 178, 442, 524, 525, 527, 531, 532; ammocoetes, 267; amphioxus, 22, 23; formation of, 162, 164, 167, 171, 172, 173, 174; tunicate, 20
Notaryctes, 61
Notosema, 771
Nototherium, 99
Nototrema, 38, 485
 Nuclease, 323
 Nucleolus, 130, 135
 Nucleoplasm, 130
 Nucleus, 129, 130; abducens, 734; ambiguus, 734, 735; cuneatus, 718, 719; dorsal motor of Xth, 735; dorsalis, 687, 691, 720, 721; Edinger-Westphal, 733; granilis, 718, 719; habenular, 507; hypoglossal, 735; inferior salivatory, 734; motor of Vth, 732; motor of VIIth, 734; oculomotor, 733; of Pander, 452; pulposus, 529; superior salivatory, 734; trochlear, 733
 Nuthatch, 57
 Nymph, 479
 Obsidian, 115
 Occipital, bone, 534, 566, 570, 580, 582; condyle, 534, 558, 559, 566, 567, 587, 589, 592
Odobenus, 66
 Odontoblast, 288, 289, 290
 Odontoceti, 79, 290, 292, 295, 313
 Odor, 773
 Oestrus, 493
 Oikos, 82
Okapia, 74
 Olfactoreceptor, 759, 772, 776
 Olfactory, bulb, 708, 712, 713, 725, 726, 733; capsule, 556, 557-559, 569; center, 716, 773; lobe, 701, 704, 712, 724, 725, 727-729, 733; membrane, 776; nerve, 712, 733, 736-738; pit, 302; sac, 557, 726; stalk, 723, 725
 Oligocene, 125
 Omasum, 309
 Omental bursa, 328
 Omentum, greater, 328, 430; lesser, 328
 Ommatidium, 806
 Omnivores, 264
 Omosternum, 549, 550
Onohippidium, 99
Orychodactylus, 237
 Oocyte, 136
 Oögenesis, 465
 Oögonia, 136
 Opening, anal, 324; atrial, 20; atrio-ventricular, 355; auriculo-ventricular, 357, 358; cloacal, 306; sinuatrial, 355; urethral, 479, 489; urogenital, 489; vaginal, 489
 Opercular, 561, 564, 575
 Operculum, 392, 393
 Ophidia, 49
Ophiocephalus, 386
Ophisaurus, 50
 Opisthocorallus, 529, 530
Opisthocornus, 238, 306
 Opisthos, 530
 Opisthotic, 567, 568, 569, 580
 Opossum, 60, 61, 214, 222, 227, 233, 297, 298, 478, 479
Opsanus, 398, 399, 401
 Opsonins, 191, 339
 Optic, capsule, 556, 557, 568; chiasma, 704, 708, 711, 723, 724, 738, 739; cup, 705, 808, 814; disc, 814; lobe, 704, 723-726, 727-729, 739, 740; nerve, 653, 708, 713, 725, 726, 733, 736-738, 739, 807, 809; stalk, 705, 808, 814; vesicle, 808
Ora serrata, 807, 810, 812, 817
 Oral cavity, 275, 277, 303, 401
 Orang utan, 69, 125, 126
 Orbit, 280, 574, 578, 579, 587
 Orbitosphenoid, 568, 580

- Orca*, 79
Orchis, 460
Order, 14
Ordovician, 103
Organ, 141; adhesive, 20; chemical sense, 772; copulatory, 473-480; of Corti, 734, 796, 797, 798, 799, 803; cutaneous sense, 760; electric, 663; enamel, 288, 289; genital, 457; gravity, 784; hydrostatic, 400; intermittent, 475; Jacobson's, 574, 778; lateral-line, 743, 769; light (luminescent), 216, 671; mammary, 222-228; parietal—see parietal body; pineal—see pineal body; pit, 769, 770; of prehension, 273; pressure, 761; reproductive, 471, 479; respiratory, 384; sense, 167, 204, 676, 753; sexual, 457; smell, 772; stato-acoustic, 784; taste, 772, 780-783; touch, 760; urogenital, 474, 479, 488; Weber's, 400, 787; wheel, 22
Organization centers, 178
Organology, 167
Orientation, 769
Origin of muscle, 647
Ornithorhynchus, 38, 59, 227, 253, 463, 622, 678
Ornithos, 54
Orohippus, 99
Oropharynx, 303, 304, 403
Orthal, 294
Orycteropus, 71, 72
Os priapi, 478
Osnonx, 298
Osphromenus, 386
Osprey, 213
Ossicles, 232
Osteichthyes, 29, 32-35
Osteo-, 29
Osteoblast, 147, 150, 151
Osteoclast, 147, 148, 150, 151
Ostium tubae abdominale, 437, 461, 468, 470, 474, 479, 485, 488
Ostraco-, 27
Ostracoderm, 27, 29, 229
Ostrich, 56, 247, 313, 477
Otic, bones, 567-569, 578, 580, 587, 596; capsule, 556, 557-559, 564, 565, 568; ganglion, 747; vesicle, 789
Otoconia, 786, 802
Otolith, 20, 787, 802
Otter, 58, 64, 307
Oudenodon, 290
Outflow, cranial, 746, 747; uveal, 746, 747; thoracic-lumbar, 746, 747
Oval, 400
Ovarian cavity, 462
Ovary, 437, 455, 460-463, 461, 465, 466, 468, 471, 474, 479, 488, 495, 499
Overpopulation, law of, 85
Overtones, 801
Ovis, 75
Oviduct, 461, 462, 468, 470, 471, 474, 479, 488
Oviparous, 472
Ovis, 75
Ovisac (ovarian sac), 461, 462, 466
Ovulation, 495
Ovule, 157, 472
Ovum—see egg
OWEN, 460
Owl, 57, 238, 270, 313, 461, 533
Ox, 316, 430; musk, 75
Oxus, 22
Oxygen, 262, 301, 302, 303, 383
Oxyhaemoglobin, 333
Pachyornis, 622
Pad, digital, 237
Paddlefish (*Polyodon*), 34
Paedogenic, 21
Pain, 692, 717, 719
Painting, 111
Palaeolith, 117, 118
Palaeolithic, 117, 118, 119, 296
Palaeomastodon, 76, 296
Palaeontological laws, 104
Palaeozoic, 103, 127
Palate, hard, 277, 302, 303, 570, 578, 579, 778; soft, 277, 303
Palatine, bone, 568, 575, 576, 578, 579, 580, 582, 587, 588; ridges (rugae), 277
Palatopterygoid, 569
Palatoquadrate, 562
Pallium, 712, 723, 724, 725
Palm, 629
Pancreas, 167, 172, 305, 306, 315, 319-322, 319, 320, 327, 430, 512; development of, 319, 320
Pangolin, 71, 121, 213, 221
Papilla, 205, 283; basal, 803; dental, 289; dermal, 205, 221, 244, 245, 250, 254, 764; esophageal, 305; feather, 244, 245; filiform, 282, 284, 285; foliate, 282, 294; fungiform, 282, 284, 285; genital, 462, 467; hair, 221, 250, 254; lingual, 284, 285, 780; nutritive, 205; renal, 431, 433; sensory, 205, 764; taste, 282, 284, 285, 781; urethral, 477; urinary, 474; urogenital, 474; vallate, 282, 284, 285
Papillary, layer, 205, 206; ridge, 250
Parabronchus, 409
Parachordal, 556, 557
Paraconid, 298
Paraconus, 298
Paradidymis, 457, 468, 487, 488
Paraganglia, 510

- Parahippus*, 99
Paramecium, 772
 Paraphysis, 507, 704, 724, 728
 Parapophysis, 522, 523, 546
 Parapsid, 584
 Parasite, 264
 Parasitology, 188
 Paraspheonoid, 575, 576, 577, 580, 587
 Parasternum, 554
 Parathyroid, 499, 500, 502
 Parietal, body (organ), 4, 507, 704, 705, 724, 728, 820; bone, 555, 561, 567, 568, 569, 574, 575, 578, 579, 581, 582, 589, 598
 PARKER, G. H., 217, 667, 672, 718
 PARKER, T. J., 30
 Paroöphoron, 468, 487, 488
Parva, 238
 Parrot, 57, 461, 530, 781, 828
 Pars, anterior, 505; distalis, 505; intermedia, 505, 506; nervosa, 505; tuberalis, 505
 Parturition, 506, 509
 Passeriformes, 57
 PASTEUR, 5, 188
 Patch, Peyer's, 314
 Patella, 633, 649
 Path, final common, 694
 Pathology, 182
 Pathways, autonomic, 747; craniospinal, 718-722
 PATTEN, 349, 350
 Paunch, 309
 Peacock, 248
 PEARL, 509
Pecari, 73
 Peccary, 73
 Pecten, 827, 828
 Ped-, 65
 Peduncle, cerebellar, 707, 710, 720, 721; cerebral, 708, 710, 713
 Peking (Peiping) man, 122
 Pelican, 56, 219, 410
 Pelvis, female, 616; renal, 431, 433, 434
 Penguin, 56, 243, 247, 330, 631
 Penis, 473, 475, 476, 477, 478, 490; bone, 478; double, 475; evolution of, 476; of man, 457, 476, 477; spines, 477
 Penta-, 627
 Pepsin, 311, 323, 327
Perameles, 60, 478
Perca, 461
 Perch, 35, 307, 461
 Perching mechanism, 635
 Percidae, 416
 Peregrini-, 41
 Perennibranchiata, 41, 281, 396, 416
 Peri, 206
 Pericardial cavity, 177, 178, 353
 Pericardio-peritoneal canal, 177, 354
 Pericardium, 353
 Perichondrium, 145, 151
 Periderm, 206
 Perilymph, 377, 795, 798
 Perimysium, 649
 Perineum, 489
 Perineurium, 676
 Periodicity in reproduction, 491
 Periods, geologic, 103
Periophthalmus, 386, 622
 Periosteum, 145, 151, 647
 Perisso-, 72
 Perissodactyla, 62, 72, 72-73, 77, 412, 431, 487, 637
 Peristalsis, 271, 751
 Peritoneal cavity, 177, 178, 354, 430
 Peritoneum, 167, 178, 271, 326, 430
 Permian, 103
Perodicticus, 241
 Pessulus, 423
 Petrel, 56
 Petrification, 100
 Petromastoid (petrosal), 568, 578, 580, 596
Petromyzon, 26, 27, 209, 319, 390, 466, 525, 584, 696, 723, 787, 820
 Petros, 26
 Petrosal—see petromastoid
 Peyer's patches, 314
 PITTNER, 633
 PELÜGER, 508
Phacochorus, 73, 299
 Phag-, 337
 Phagocyte, 337
 Phalanges, 607, 627, 629, 632, 638
 Phallus, 478, 489
Phallusia, 389
 Pharyngeal breathing, 10
 Pharyngo-branchial, 280, 563
 Pharyngo-esophageal network, 386
 Pharynx, 19, 301-304, 401, 735
Phascogaster, 61
Phascogaster, 61
 Phenyl-thiocarbamide, 783
 Philology, 109
 Phileas, 336
Phoca, 66
Phocarpa, 79
 Pholidota, 62, 71
Pholidotus, 71
 Phonoreceptor, 759, 788-804
Phoronis, 333
 Photoreceptor, 22, 759, 804-830
 Photosynthesis, 600, 601
 Phototropic, 805
 Phrenology, 715
Phrynosoma, 50, 51, 233, 234, 374
 Phyla, 14

- Physeter*, 79
 Physiology, 182
Physoclisti, 398
Physostomi, 398
Pia mater, 585, 698, 699, 705
Pickerei, 35, 398
PICKET, 104
Pig, 73, 405, 420, 762, 775; digestive system, 285, 297, 316; foot, 637; integument, 222, 223, 225, 252; reproductive system, 480, 481, 487
Pigeon, 57, 245, 248, 306, 313, 334, 410, 461, 506, 536, 569, 589; passenger, 96
Pigment, 204, 205, 210, 256; cup (shield), 806, 821
Pike, 293, 438
Pile dwellings, 110
Pilocarpin, 750
Pittdown, 123-124, 125, 127
Pineal body (gland), 499, 507, 705, 707, 708, 710, 711, 724, 728, 729, 820
Pinna, 65, 395, 788, 789, 790, 792, 803
Pinnipedes, 65, 66, 404
Pipa, 38, 43, 282, 396
Pipefish, 232, 290, 325, 398, 399, 485
Pisces, 17, 27-35
Pisiforme, 627, 628
Pit, auditory, 791; nasal—see pit, olfactory; olfactory, 302
Pitch, 801, 802
Pithecanthropus, 120-122, 124, 125, 126, 127
Pituitary—see hypophysis
Pituitrin, 505
Placenta, 45, 61, 351, 486, 499
Placental, 61, 484
Placode, epibranchial, 732
Plane, frontal, 8; sagittal, 8, 593; transverse, 8
Plant, 498
Plantigrade, 603, 637
Plasma, 339
Plastron, 48, 621
Plate, alar, 686, 687; basal, 686, 687; costal, 533; cribriform, 569, 570, 593, 738; embryonic, 174, 175; end, 668; floor, 675, 685, 686; medullary—see plate, neural; mesothelial, 353; neural, 161, 162, 172, 173, 527, 533, 674, 675; perpendicular of ethmoid, 582, 592; roof, 685, 686; tarsal, 818, 819
Platy-, 68
Platyrrhines, 68, 297
Plectrum, 794
Pleistocene, 125
Plesiosaur, 45
Pleura, 402, 413
Pleuracanthus, 609, 610
Pleural cavity, 177, 178, 413
Pleurocentrum, 528, 529
Pleurodont, 293
Pleuronectidae, 397, 438, 460
Plexus, Auerbach's, 673; brachial, 681, 684; cardiac, 750; cervical, 684; cervico-brachial, 685; choroid, 705; choroid, anterior, 710, 711, 728; choroid, posterior, 707, 710; coeliac, 510, 750; hypogastric, 750; lumbo-sacral, 681, 684; Meissner's, 673; solar, 750
Plica semilunaris, 818, 819
Plicae circulares, 268
PLINY, 27
Pliocene, 125
Pliohippus, 99
Pliohylobates, 125
Pliopithecus, 125
Plover, 37
Plumage, 246; colors, 248, 508
Pneum-, 33
Pocket, milk, 225, 226; subcephalic, 349
Pod, 36
Polarity, 667
Pole, animal, 159, 168, 169; vegetal, 158, 168, 169
Polistotrema, 442
Pollen, 157, 472
Poly-, 34
Polycanthus, 386
Polydactylum, 633
Polyodon, 34, 230, 545
Polyoestrous, 493
Polyphyodont, 291
Polypterus, 34, 230, 268, 312, 396, 395, 406, 545
Pomum Adami, 423
Pons, 681, 701, 708, 709, 710, 711, 713, 719, 720, 721, 722, 725, 730
Porcupine, 66, 67, 196, 252, 420
Pore, abdominal, 466, 467, 474; atrial, 19, 20, 22, 389, 466; femoral, 218; genital, 462; sweat, 205; taste, 780, 781; urinary, 462, 467; urogenital, 467
Porpoise, 79, 430
Postcleithrum, 575
Posterior, 8, 9
Postfrontal, 574, 578, 581
Postorbital, 561, 574, 578, 579, 581
Postparietal, 561, 578
Posttemporal, 561, 575, 619
Postzygapophysis, 523
Pouch, branchial, 387, 388, 500; cheek, 276; gill, 387, 388, 500; marsupial, 59, 60; mesodermal, 176; pharyngeal, 387, 388; Rathke's, 166, 318, 505, 506
Prairie dog, 66, 67
Precartilage, 146

- Prechordal, 556, 557
 Precocial, 247
 Prefrontal, 574, 578, 579, 581
 Pregnancy, 493, 494, 552
 Prehension, 272, 273
 Premaxillary, 561, 568, 569, 574, 575, 578, 579, 581, 587, 588, 589
 Premolar, 295
 Preopercular, 561, 564, 575
 Prepuce (Preputium), 457, 476, 477, 489, 490
 Presphenoid, 568, 580
 Pressure, 717, 719, 760; blood, 506
 Prevomer, 569, 575, 576, 577, 580
 Prævostr, 453
 Prezygapophysis, 523
 Primates, 62, 67-70, 68, 69, 92, 225, 240, 376, 480
 Primitive streak, 171, 172, 174, 175, 349
 Prints, finger, 259, 260
Prionotus, 397, 401
 Priority, law of, 16
Prinia, 31, 299, 585
Pristiurus, 443
 Pro, 530
 Proboscidea, 62, 75-76, 76, 77, 412
 Proboscis, of elephant, 76; of hemichordate, 17
Procapra, 77
 Procellariformes, 56
 Process, acromion, 621; ascending of pterygoquadrate, 570, 573; basal of pterygoquadrate, 564, 565, 573; ciliary, 810, 817; coracoid, 621, 622, 628; entoglossal, 571, 576; epipubic, 610; falciform, 823; iliac, 610; mastoid, 577, 596; nasal, 775; odontoid, 534, 535; otic of pterygoquadrate, 564, 565, 573; pectineal, 614; prepubic, 610, 612, 614; pterygoid, 582; styloid, 572, 577, 578, 596; transverse, 523; uncinat, 547, 548; urothral, 477; vaginal, 459; xiphoid, 532, 553
 Processus vermiformis, 269, 313
 Procoracoid, 549, 607, 608, 609, 620, 621, 628
 Proctodærum, 166, 167, 270
Procyon, 64
Proechidna, 58, 59
 Progesterone, 509
 Pronation, 632, 649
 Pronephridia, 441, 442, 466, 468
 Pronephros, 440, 441, 442, 466
 Pronghorn, 75, 236
 Prootic, 568, 569, 580, 587
 Propional, 274
 Prophase, 134, 135
Propliopithecus, 125
 Proprioceptive sense, 717, 719
 Proprioceptor, 758, 759, 785, 830
 Propterygium, 609, 619
 Propyl-mercaptan, 773
 Prosencephalon, 349, 703
 Protandrous, 463
 Protase, 327
 Protection, 196, 197, 517, 518, 525
 Protein, 265, 314, 323, 327
 Proterozoic, 102, 103
Proteus, 334, 396, 530, 548, 610
 Prothrombin, 339
 Proto-, 58
 Protocecal, 623, 624
 Protochordate, 17
 Protoconid, 298
 Protoconus, 298
Protohippus, 99
 Protonephridium, 440, 441
 Protoplasm, 601
Protopterus, 33, 395, 406, 610
 Prototheria, 58-59
 Protzoa, 207, 273, 428; pathogenic, 187
 Protozoology, 188
 Proventriculus, 306, 310
Pseudacris, 43
 Pseudobranch, 392
 Pseudohypertrichosis, 257
 Pseudopod, 273
Pseudopus, 626
 Pter-, 34
Pteranodon, 290
Pterichthys, 27
 Ptero-, 47
 Pterodactyl (pterosaur), 201, 630
Pterodactylus, 46
 Pteropods, 273
 Pterosaur, 47
 Pteryg-, 33
 Pterygoid, 567, 568, 576, 578, 579, 580, 582, 587, 588
 Pterygoquadrate, 280, 562, 564, 565, 572
 Pterylic, 247
 Pyralin, 276, 323, 327
 Pubis, 532, 548, 607, 608, 609, 610, 611-616, 628
 Pulmonary, aorta, 358, 361, 366, 367, 368; artery, 200, 343, 355, 357, 358, 361, 366, 367, 368, 406; vein, 343, 355, 357, 361, 373, 406
 Pulp cavity, 287, 288, 289
 Pulvinar, 733
 Punctum, fixum, 647; lacrimale, 818, 819; mobile, 647
 Pupil of eye, 810, 825
 Pus, 338
Pygopus, 626
 Pygostyle, 534, 536

- Pyloric, caecum, 268, 269, 312; region of stomach, 307, 308
 Pylorus, 307, 308
 Pyramid, of brain, 707, 708, 710, 720, 722; decussation, 708, 709, 710, 720, 722; Malpighian (renal), 431, 434
 Python, 404, 408, 531, 613, 626
 Quadrate, 564, 565, 567, 569, 572, 573, 574, 575, 576, 579, 580, 582, 587, 588, 589
 Quadratojugal, 567, 574, 576, 578, 579, 580, 587, 589
 Quail, 57
 Quarternary, 103
 Quartz, 115
 Quill, 243
 Rabbit, 174, 175, 220, 269, 312, 316, 334, 420, 460
 Raccoon, 54, 65
Rachianectes, 79
 Radiale, 627, 628
 Radialia, 605, 609, 619, 624
 Radio-ulnar, 627
 Radius, 607, 627, 628, 631, 632
 Radix aortae, 365
Rais, 31
 Rail, 57
 Rakers, gill, 391, 392, 395
 Ramus, communicans, 749; gray, 745, 748, 749; interganglionic, 749, 750; transversarius, 750; white, 745, 748, 749
 Rana, 43, 218, 379, 395, 422, 471, 530, 532, 549, 550, 576, 587, 611, 825
 RAN, 175, 613, 653
Rangifer, 75
 RANSON, 686, 694, 709, 712, 716, 717
 RANVIER, 204
 Raphe, 277, 282, 489, 490
 Rat, 65, 214, 220, 233, 253, 256, 420
 Rate of living, 261
 Rathke's pouch, 166, 318, 505, 506
 Ratitae, 55-56, 238, 477
 Rattlesnake, 51, 52, 279, 420, 588; rattle, 241, 242
 RAUBER, 202
 Rays, 31, 230, 392; branchiostegal, 395; fin, 609, 619; gill, 280
 Receptor, 670, 754, 755, 758; olfactory, 759, 772, 776; temperature, 764
 Rectum, 305, 324, 325, 479, 490; vascular, 386
 Reflex arc, 670, 694; somatic, 745; visceral, 745
 Region, olfactory, 776; respiratory, 776; vestibular, 775
 Regurgitation, 304, 309
 Reindeer, 75, 112, 127, 235, 236
 Relayer, 670, 671
 Renal, artery, 431, 434; calyx, 431, 433; corpuscle, 432; cortex, 431, 434, 435; lobule, 435; medulla, 431, 435; papilla, 431, 433; pelvis, 431, 433, 434; portal vein, 342, 343, 371, 372, 373, 374, 375; pyramid, 431, 434; vein, 375, 376, 431, 434
 Rennin, 311, 327
 Repere, 43
 Replacing bone, 150, 151, 561, 580, 581
 Repression, 84, 89
 Reproduction, 5, 447; asexual, 156, 448; sexual, 136, 156, 448
 Reptile, air sacs, 387; aortic loops, 366, 367; appendages, 603, 625, 627, 630, 631; brain, 724, 728; breathing, 417; chromatophores, 217; claws, 237; colic caecum, 269; copulation, 473, 475; development of, 169-173; dog-toothed, 45; egg, 159, 452-454; epidermal glands, 218; epiphysis (pineal body), 507; extinct, 45-47, 518, 702; fetal envelopes, 44, 486; flying, 47, 49, 201; golden age of, 45, 103; hard palate, 302; heart, 355, 358; integument, 212, 213, 218, 232; intestine, 312; jaws, 564, 576; lungs, 408; lymph hearts, 379; mammal-like, 45; meninges, 699, 700; mesonephros, 445; metanephros, 445; mouth glands, 279; muscles, 654, 655, 656, 660; nerve cord, 698; occipital condyles, 567; ovary, 461, 463; parathyroid glands, 502; parietal organ, 507; pectoral girdle, 620, 621; pelvic girdle, 612-614; penis, 476; ribs, 545, 546, 547; scales, 212, 232; sense organs, 761, 774, 777, 778, 779, 781, 788, 794, 803, 825, 828; skull, 565-582, 567, 574, 578, 579, 587, 588; stem, 47; sternum, 550, 551, 552; teeth, 292, 293; thymus gland, 503, 504; thyroid gland, 500; trachea, 404; tongue, 282; urinary bladder, 438; urine, 436; urogenital ducts, 468, 469; veins, 374, 375; vertebrae, 528, 530, 533, 534; voice, 420
 Reptilia, 17, 38, 43-52
 Resonance sac, 422, 425
 Respiration, 200; amphibian, 57, 200, 385; branchial, 344; external, 384; fishes, 29; internal, 384; pulmonary, 344
 Respiratory surface, 402
 Response, 756
 Rete, mirabile, 399, 434; testis, 457, 458, 469, 487, 488
 Reticulum, 309
 Retina, 807, 808, 811, 812; inversion of, 814, 815
 Retroperitoneal, 430

- Rh factor, 69
Rhazaphorus, 38
Rhea, 56, 615
 Rheoreceptor, 759, 769
 Rhesus monkey, 69
 Rhin-, 68
 Rhinencephalon, 712
Rhinoceros, 72, 73, 234, 249, 460; woolly, 96, 112, 124
Rhinoderma, 38, 485
Rhinodon, 27
 Rhodopsin, 813
 Rhombencephalon, 349, 703
 Rhynchocephalia, 48
Rhytina, 78
 Rib, 178, 521, 522, 533, 539, 542-548; abdominal, 554; breathing, 418; dorsal, 521, 545, 546; extra, 544, 545; false, 543; floating, 543; gorilla, 544; haemal, 545, 546; human, 542, 543; lumbar, 544, 545; sacral, 535, 610, 611; true, 543; ventral, 521, 545, 546
 RIDDLE, 506
 Ridge, friction, 205, 257; genital, 455, 456, 460, 464, 489; palatine, 277; papillary, 258; sublingual, 278
 Right-handedness, 646
 Ring, tracheal, 404, 424, 425, 571; tympanic, 578, 596
 Ritter, 18
 Rock rabbit, 77
 Rocks, sedentary, 101
 Rodent, cerebrum, 714; cheek pouches, 276; cecic caecum, 269, 313; epiphysis, 730; kidney, 431; nipples, 222, 225; reproductive system, 477, 478, 480, 481; teeth, 288, 292, 294, 295, 299; veins, 376
 Rodentia, 62, 65-66, 67
 Rods, 808, 811, 812
 Roof, of mouth, secondary, 579
 Root, dorsal, 680, 682, 683, 690; hairs, 263; motor, 682; of nerves, 684; sensory, 682; of tooth, 287; ventral, 680, 682, 683, 686, 690
 Röss, 298, 300
 ROSENBERG, 632
 Rostrum, 22, 280, 299, 558, 585
 Rotation, 649
 Rotifers, 273
 Rouget cells, 347, 348
 Rugae, palatine, 277; vaginal, 479
 Ruven, 309
 Ruminants, 73-75, 74, 75, 220, 222, 223, 225, 296, 304, 309, 405, 473, 477, 481, 487
 Ruminare, 73
 SABIN, 377, 380
 Sac, air, 387, 408-410; alveolar, 401, 405; auditory, 791; brood, 485; cloacal, 386; cochlear, 796; endolymphatic, 792, 797; gill, 391; lymph, 379; olfactory, 557, 726; ovarian, 461, 462, 466; preputial, 476; resonance, 422, 425; scrotal, 459, 476, 478, 480, 490; siphon, 474; vocal, 422; yolk, 44, 166, 172, 173, 174, 486
 Sacculus, 734, 786, 791, 792, 795, 796, 798
 Saccus vasculosus, 723, 726
 Sacrum, 535, 537
 Sagittal plane, 8
 Salamander, 40, 41, 237, 281, 282, 372, 388, 611; body muscles, 654; lungless, 386, 407
Salomandra, 41, 281, 438, 442, 475, 611
Salamandrina, 407
 Salientia—see *unura*
 Saliva, 276
Salmo, 823
 Salmon, 35, 307, 492
 Salmonidae, 290
 Salts, bile, 315
 Salty, 782
 Sand-lance, 312, 461
 Sandpiper, 57, 763
 Saprozoa, 264
 Sarcoplasm, 152
 Saur-, 47
 Sauropsida, 44
 Sawfish, 31, 299, 585
 SAYLES, 243, 369, 415, 474, 550, 558, 569, 576, 650, 713, 770
 Scala, media, 798; tympani, 797, 798; vestibuli, 797, 798
 Scales, amphibian, 212, 232; bird, 213, 233; ctenoid, 229, 231; cycloid, 229, 231; fish, 211, 229; ganoid, 229, 230; mammalian, 213, 214, 233; placoid, 229, 290; reptilian, 212, 232, 243
Scalopus, 63, 292
Scapanus, 63
Scaphiopus, 42
Scaphirhynchus, 34, 230
 Scaphoid, 628
 Scapula, 404, 541, 548, 550, 575, 607, 608, 609, 618, 619-622, 628
 SCHUCHZER, 120
 SCHIMKEWITSCH, 308
 Schizo-, 176
 Schizococle, 176
 SCHLEIDEN, 129
 SCHUMANN, 702
 SCHWANN, 129
 Sciaenidae, 400
 Scientific name, 15
Sciuropterus, 65, 67

- Sciurus*, 65, 67
 Sclera, 145, 569, 807, 809, 817
 Sclero-, 165
 Scleroblast, 231
 Sclerotic, 568, 569, 827, 828; coat, 145, 569, 807, 809, 817
 Sclerotomes, 165, 526
Scomber, 268, 312, 624
 SCOTT-ELLIS, 118
 Scrotum, 459, 476, 478, 489, 490
Scyllium, 453, 565, 606, 774
Scymnognathus, 45
 Sea, anemone, 265; bass, 463; cow, 77, 78, 224, 249, 254, 299, 404, 534, 548; cow, Steller's, 78, 96; cucumber, 12; horse, 232, 290, 485; lion, 65, 66; robin, 397, 401; squirt, 18; urchin, 265
 Seal, 65, 66, 198, 307, 430, 470, 478, 480, 492
Sebastopristis, 28
 Sebium, 220
 Secretin, pancreatic, 322
 Secretion, 143, 200
 Segmentation, cavity, 160, 161, 164, 168, 169, 170, 176, 178; intestinal, 271
 Segment, 9
 Selachii, 30, 229, 299, 354
 Selenodont, 296
 Sella turcica, 504, 570, 592
 Semen, 482
 Semilunar, 628
 Seminal vesicle, 457, 469, 474, 481
Semnopithecus, 308
 Sensation, 199
 Septomaxillary, 574, 579, 581, 778
 Septum, 9; branchial—see septum, gill; dorsal connective tissue, 178, 521, 522, 523; dorsal, of nerve cord, 680, 687, 688; dorsal intermediate, of nerve cord, 691; gill, 388, 391, 392, 394; horizontal, 178, 521, 522, 654; interauricular, 356, 357; interorbital, 587; interventricular, 358, 361; nasal, 570, 733, 819; pellucidum, 708, 714; transversum, 177, 318, 354, 413, 657; ventral, 178, 521, 522, 650
 Serena, 271, 306, 326, 328
 Serpent, 51
Serranus, 463
Serricomer, 28
 Sesamoid, 628, 633, 649
 Sex, determination of, 138, 139, 489; differentiation of, 489; characters, secondary, 456
Seymouria, 45, 578
 Shaft, feather, 243, 244; hair, 221, 254
 Shank, 628
 Shape of sound waves, 801
 Shark, 30, 229, 291, 392, 453
 Shreath, 145; hair, 221, 250, 254; medullary, 668, 669; myelin, 668; notochordal, 144, 524, 527; Schwann's, 668
 Sheep, 75, 236, 252, 297, 420, 477
 Shell, egg, 451, 452, 453, 485; heaps, 110
 SHERRINGTON, 694, 758, 768
 Shield, embryonic, 175
 SHIPLEY, 153
 Shore birds, 57
 Shoulder, 628
 Shrew, 62, 63, 220, 233, 481
 Sight, 715, 717, 785, 804
 Silurian, 103
 Siluroid, 229, 400
Simia, 69
 Simiidae, 69
Sinanthropus, 122
 Sineu, 648
 Sinus, coronary, 377; ethmoid, 593; frontal, 303, 582, 593, 594; mastoidal, 596, 791; maxillary—see antrum; rhomboidal, 349; sphenoidal, 303, 582, 592; urogenital, 466, 476, 478, 479; venous, 354-357, 363
 Siphon sac, 474
Siphostoma, 398, 399
Siren, 290, 396, 421, 625
 Sirenia, 62, 77-78, 78, 92, 220, 221, 412, 625
 Sirens, 77
 Skate, 30, 31, 230, 392, 545
 Skeleton, 167; appendicular, 521; axial, 521, 525; locomotor, 600; uses of, 517
 Skin—see integument
 Skin-brain, 703
 Skull, 521; *Acipenser*, 560; alligator, 567; *Amia*, 561; amphistyle, 564, 565; auto-style, 564; bird, 589, 590; bones, 580, 581; composite, 568; cotylosaur, 578; craniostyle, 564, 565; cyclostome, 584; deformation of, 597, 598; dogfish, 280, 558; dolphin, 598; frog, 588; ganoid, 560, 561; human, 565, 570, 578, 582, 592; hystyle, 564, 565; lizard (*Varanus*), 579; mammalian, 568; *Necturus*, 569; *Sphenodon*, 574; *Squalus*, 280, 558, 562; teleost, 575; turtle, 567, 579
 Skunk, 65, 197, 222, 297, 483
 Sleeping sickness, 188
 Slits, gill, 12, 302, 387, 388
 Slosson, 338
 Sloth, 70, 71, 99, 221, 239, 252, 404, 534, 547
 Slow worm, 30
 Smallpox, 191
 Smegma, 483
 Smell, 199, 772
 Smeit, 307

- Sminthopsis*, 60
 SMITH, G. E., 125
 SMITH, P. E., 763, 807, 812
 SMITH-WOODWARD, 123, 124
 Snake, 43, 49-52, 52, 438; digestive system, 274, 282, 305, 307, 318; molting, 197; reproductive system, 456, 461, 463, 473, 475; respiratory system, 405, 408, 420; skeleton, 539, 549, 613, 625, 685; teeth, 292, 293, 294, 300; veins, 374
 Snout, 775
 Sole, 307, 629
 Solenocyte, 441
 Solomon, King, 420
 Solutrfan, 118, 119
 Soma, 180
 Somatic mesoderm, 162, 164, 172
 Somatoplasm, 447, 454, 455, 464
 Somite, 165, 172, 349
 Sorex, 63
 Sound, production of, 400; waves, 801
 Sour, 782
 Space, epidural, 699; of Fontana, 816; perimeningeal, 699; subarachnoidal, 699; subdural, 699; temporal, 583
 SPALLANZANI, 790
 Sparrow, 57
 Species, 14; number of, 3
 SPEMANN, 179
 SPENCER, 4
 Sperm, 136, 157, 158, 472; cells, 132, 136, 449-451, 449, 458, 472; groove, 476; human, 159; typical, 132; viability, 450
 Sperma, 449
 Spermatid, 481; cord, 459
 Spermatid, 136, 458
 Spermatocyte, 136, 458
 Spermatogenesis, 458, 464
 Spermatogonium, 136, 458, 464
 Spermatophore, 475
 Spermatozoa, 132, 136, 449-451, 449, 458
Sphaeroides, 397
 Sphenethmoid, 587
 Sphenisciformes, 56
Sphenodon, 4, 43, 48, 825; digestive system, 292, 298, 300; lungs, 407, 408; parietal eye, 507, 820; scales, 233; skeleton, 536, 547, 554, 574, 612, 627
 Sphenoid, 505, 555, 561, 570
 Sphincter, 649; anal, 325, 649; marsupial, 662; pupillae, 811, 817
Sphyryna, 822
 Spiders, 273
 Spinal, cord—see nerve cord; curvatures, 538; frog, 731
 Spindle, 135
 Spine, fin, 624; haemal, 475, 522, 323; integumentary, 252; neural, 521-523, 525; of penis, 477; scapular, 623
 Spiracles, 303, 391, 392, 393, 395, 565, 573, 789
 Spiral valve, 268, 312
 Spireme, 134, 135
 Splanchnic mesoderm, 162, 164, 172
 Splanchnocranium, 280, 555, 562, 572, 573
 Spleen, 337, 380
 Splenial, 576, 579, 581
 Sponge, 265, 273, 340
 Spongioblast, 685, 686
 Spoon-bill, 34, 230
 Spur, 242; of clasper, 474
 STURZENHEIM, 715
Squalus, 31, 280, 355, 474, 511, 558, 609, 619, 726, 769, 770
 Squama, of temporal, 570, 578, 595
 Squamata, 48, 49-51
 Squamosal, 561, 565, 567, 568, 569, 574, 576, 578, 579, 580, 582, 587, 588, 589
 Squeteague, 400, 401
 Squirrel, 65, 67, 250, 276, 285, 297, 760
 Stag, 473, 508
 Stage, independent effector, 672; receptor-effector, 672
 STAHR, 782
 Stalk, allantoic, 318; olfactory, 723, 725; optic, 705, 808, 814; yolk, 166, 173, 318
 Stapes, 571, 572, 573, 581, 583, 791-794, 798
 Starfish, 265, 274
 Statocyst, 785
 Statolith, 785
 Statoreceptor, 785
 Steapain, 321, 323, 327
 Steatopygy, 480
 Stegocephali, 39-40, 40, 528, 545, 554, 567, 611, 620
 Stegos, 40
Stegosaur, 46, 613, 614, 677
 STEINACH, 508
Stenodon, 121
 Stenor, 772
 STEPHAN, 773
Sterna, 291, 630, 631
 Sternal part of rib, 547
 Sternebra, 551, 552, 622
Sternoptys, 28
 Sternum, 404, 519, 521, 539, 540, 541, 548-554, 609
 Stickleback, 325, 453, 780
 STILES, 714, 754
 Stimulation, electrical, 689
 Stimulator, 760-763
 Stimulus, 665, 754; chemical, 759; mechanical, 759; radiant, 759
 Stirrup, 583
 Ströma, 131

- Stoma, 25
 Stomach, 269, 305, 306-311, 307, 430;
 cardiac region, 307, 308; functions of,
 310; glandular, 310; honeycomb, 309;
 hour-glass, 308; human, 307; manyplics,
 309; ruminant, 309
 Stomodaeum, 166, 167, 270, 504
 Stonehenge, 113, 114
 Stork, 56, 420
 Stratum, corneum, 203, 204, 205; granu-
 losum, 203, 204; lucidum, 203, 204, 240;
 Malpighii, 203, 204, 205
 Streak, primitive, 171, 172, 174, 175, 349
 Streams, hair, 251, 252
Struthio, 615
 Surgeon, 34, 230, 290, 307, 312, 321, 560
 Stylohyal, 568, 577
 Subcutaneous, 203, 205, 206
 Sublingual, duct, 276; gland, 276, 278, 734;
 ridge, 278
 Submucosa, 270, 271
 Subopercular, 564, 575
 Suborbital, 561, 575
 Subphylum, 17
 Substance, gray, 686, 694, 695, 696; nig-
 roid, 669; white, 686, 695
 Subunguis, 237, 238, 240
 Succus entericus, 322
 Sucking disc, 217
 Sulcus, 714; central, 714; dorsal, 687;
 limitans, 675, 686; naso-labial, 775; of
 rib, 543; terminalis, 282, 283; tympanic,
 791
 Superior, 8
 Supernumerary nipples, 227
 Supination, 632, 649
 Support, 518, 525
 Supra-angular, 576, 579, 581
 Supracleithrum, 575, 619
 Supraoccipital, 566, 567, 568, 575, 578,
 579, 580, 592, 598
 Suprarenals, 509
 Supracapula, 550, 609, 620
 Surface, auricular, 616; digestive, 266; res-
 piratory, 402
Sax, 73
 Suspension of jaws, 564, 582
 Sutures, interlocking, 520; lambdoidal, 597;
 of Mendosa, 591, 592; metopic, 593, 594;
 overlapping, 520; sagittal, 593; squa-
 matal, 520
 Swallow, 57, 827
 Swallowing, 424
 Swan, 56, 274, 403, 404, 685
 Sweat, 199, 205, 219
 Sweet, 782
 Swellfish, 397
 Swift, 57, 238, 828
 Swim (air) bladder, 387, 397-401, 397-
 399, 462, 787
 Swine—see pig
 SWINGLE, 512
 Symbiont, 264
 Symmetry, bilateral, 7; planes of, 8; radial,
 7; spherical, 7
 Sympathetic trunk, 747, 748, 749
 Sympathoblast, 510
 Symphysis, ischiaticum, 612, 613, 615; pu-
 bis, 490, 612, 615, 616
 Symplectic, 575
 Synapse, 155, 667
 Synapsid, 583
 Synarthrosis, 520
 Syndactylism, 633
Syngnathus, 232, 325, 485, 545
Synotus, 63
 Synovial fluid, 521; membrane, 520
 Synsacrum, 533, 536, 547
 Syrinx, 422, 423, 504
 System, 141; acoustico-lateral, 769; auto-
 nomic nervous, 676, 744-752, 747;
 azygos, 376; central nervous, 676; cir-
 culatory, 167; connective tissue, 521;
 digestive, 167, 261-328; excretory, 167,
 427; haemal, 340; hepatic portal, 11,
 24, 317, 342, 343, 369, 371, 373, 375,
 376; involuntary, 676, 744-752, 747;
 lateral-line, 769, 770, 771; lymphatic,
 340, 346; nervous, 10, 162, 167; para-
 sympathetic nervous, 747, 751; peripheral
 nervous, 676; portal, 11; renal portal,
 342, 343, 371, 372, 373, 374, 375; repro-
 ductive, 447; respiratory, 167; spino-
 cerebellar, 690; spinothalamic, 690;
 sympathetic nervous, 510, 747, 751;
 urogenital, 446; venous, 341, 344, 345,
 368-377
Tachycineta, 827
 Tadpole, 266, 267
 Tail, diphyccercal, 624; of fish, 624; hetero-
 cercal, 623, 624; homocercal, 623, 624;
 human, 11, 537; of monkey, 258; post-
 anal, 11; protocercal, 623, 624; respira-
 tory, 386; of tunicate, 19; types of,
 623, 624; uses of, 539
 Talon, 238
 Talonid, 299
 Talus, 628, 638, 639
Tamandua, 70, 534
 Tangoreceptor, 759, 760, 763, 785
 Tapetum lucidum, 822, 829
 Tapeworm, 311
 Tapir, 72, 460, 637
Tapirus, 72
 Tardenoisian, 118, 119

- Tarentola*, 49
 Tarsal, 607, 627, 629
 Tarsale, 629
 Tarsioidca, 68
Tarsius, 68
 Tarso-metatarsus, 635
 Taste, 199, 772, 780-783
Taxidea, 64
 Taxonomy, 13, 15
 TAYLOR ("BLT"), 678
 Tears, 819
 Tectum synoticum, 559, 586
 Tegmentum, 710, 711, 725
 Tel(e)-, 35, 159
 Telencephalon, 703, 704
 Teleost, brain, 723, 727; digestive system, 269, 312, 319; gills, 392; heart, 356; reproductive system, 456, 461, 462, 466, 470, 475, 484; scales, 231; skull, 575, 585
 Teleostei, 28, 34, 35
 Telocoels, 705
 Telolecithal, 159
 Telophase, 134, 135
 Temperature, 717, 719, 764; regulation, 411
 Temporal, 555, 570, 582, 595
 Tendon, 145, 647, 648; of Achilles, 648, 649
 Teniae coli, 325
 TENNYSON, 492
 Tetata, 184
 Teratology, 184
 Tern, 57, 630, 631
Terrapene, 49
 Tertiary, 103
 Testis, 455, 456-460, 459, 464, 466, 467, 468, 471, 474, 478, 481, 488, 490, 499, 508; descent of, 458, 459
 Tetanus, 187
 Tetra, 36
Tetrao, 219
Tetraodon, 28
 Tetraonidae, 238
 Tetrapod, 36
 THACHER, 604
 THACKERAY, 702
 THADANI, 291
 Thalamus, 707, 711, 719, 724, 728, 729; optic, 710, 739, 740
Thalassarchos, 65
Thalassochelys, 48
Thamnophis, 51
 Thecodont, 293
 Thenar, 258
 Theory, cell, 129; concrescence, 298; differentiation, 298; fin-fold, 23, 30, 604; gill-arch, 604; neuron, 666
 Ther-, 58
 Therapsid, 45, 47, 295, 567, 621
 Thermoreceptor, 764
 Thigh, 628
Thiopsis, 36
 Thirst, 262, 831
 Thoracic, basket, 539, 540, 543; cavity, 178
 Thorax, 5
 Thrombin, 339
 Thrombocytes, 338
 Thrombus, 338
 Thrush, 57, 423
 Thumb, glandular, 218, 473; opposable, 635, 640
Thylacinus, 61
 Thynius, 499-504
Thyone, 12, 333
 Thyrohyal, 568, 577
 Thyroid, cartilage, 423, 424, 425, 571, 572, 577, 578; gland, 26, 281, 390, 499-502, 504
 Thyroxin, 501
 Tibia, 607, 628
 Tibiale, 627, 628
 Tibio-tarsus, 635
 TIDEMAN, 826
 Tiger, saber-toothed, 96
 Timbre, 801
 Time scales, 102, 103, 127
 Tinamiformes, 57
Tinamou, 57, 477
 Tissue, 141; adipose, 145; bone, 148-150; cartilage, 132, 145, 146, 150; connective, 141, 143, 521; endocrine, 143; epithelial, 141, 142; erectile, 477, 480; fibrillar, 145; fluid, 141; gelatinous, 143; glandular, 143; muscle, 141, 152-154; nerve, 141, 154; notochordal, 144; reticular, 144, 145; supporting, 143, 145-152; tonsillar, 304
 Toad, 38, 42, 765; digestive system, 273, 279, 282, 290, 305, 307; horned, 50, 51, 233, 234, 374; integument, 197, 237; reproductive system, 451, 456, 463; respiratory system, 403, 406, 407, 420, 422; spadefoot, 42
 Toadfish, 398, 399, 401
 Toe, 629
 Toibr, 488
Tolypeutes, 71
 Tome, 165
 Tongue, 273, 278, 279, 280-287, 303, 734, 735; cyclostome, 280; dorsum of, 282; glandular, 281; human, 282, 285, 286; primary, 280, 281; protrusible, 282; secondary, 281, 285; woodpecker, 283, 284
 Tongue-tied, 278
 Tonals, 304; intestinal, 314; lingual, 282,

- 283, 304; palatine, 277, 282, 304, 500;
pharyngeal, 304
- Tonus, 644
- Tools, 114
- Tooth, 229, 287-301, 598; attachment of,
293; canine, 287, 295; caries of, 300;
carnassial, 295, 296; cheek, 295; corneal
egg, 300; crown of, 287, 289; cutting
of, 289, 290, 292; of cyclostomes, 209,
290; decay of, 300; development of, 288,
289; differentiation of, 294, 598; egg,
300; eruption of, 289, 290, 292; hinged,
293; horny, 209; milk, 290; molar, 298;
movement of, 294; neck of, 287; number
of, 290; permanent, 290; root of, 287,
289; situation of, 292; structure of, 287;
succession of, 291; trend of, 300; tritu-
bercular, 298; unusual, 299; wisdom, 292
- Tori, 258
- Tornaria, 18
- Torpedo, 31, 443, 453, 663, 723, 727, 771
- Tortoise, 48, 476
- Toucan, 247
- Touch, 199, 275, 692, 717, 719, 760
- Towers, 399, 401
- Toxin, 187
- Trabeculae, 556, 559
- Trachea, 385, 401, 402, 403, 404, 413, 414,
423, 541, 735
- Tracheae, 200
- Tracheal, cartilages, 404, 421, 424, 571,
572; rings, 404, 424, 425; tubes, 385
- Tract, 676, 688; ascending sensory, 689,
690; association, 690, 693; of Burdach,
689; cortico-spinal, 692, 693, 694, 698,
709, 711, 718, 720, 721, 722; descending
motor, 690, 692; of Goll, 689; olfactory,
708, 712, 713, 726; optic, 708, 738, 739,
740; pyramidal, 690, 693, 695, 713, 720,
722; spinocerebellar, 690, 691, 692, 695,
718, 719, 720, 721; spinothalamic, 690,
691, 692, 695, 718, 719, 720
- Tragic, 398
- Tragulus, 74, 253, 334
- Tragus, 789
- Transmitter, motor, 670; sensory, 670
- Transpalatine, 567, 576, 578, 580, 588
- Transverse, plane, 8; septum, 177
- Trapezium, 629
- Trapezoid, 629
- Tree shrew, 62, 63, 68
- Trema-, 58
- Tremblay, 602
- Triassic, 103
- Triceratops, 46, 233
- Trichechus, 78, 313, 534, 548
- Trichman, 206
- Trichogaster, 386
- Triconodon, 298
- Trigonidae, 460
- Trilith, 113
- Trionyx, 290
- Triquetrum, 628, 632
- Triton, 41, 42, 281, 396, 438, 463, 471, 475
- Tritubercular, 298
- Triturus, 475
- Trophoblast, 174, 175
- Trout, 35
- Truncus arteriosus, 355
- Trunk, elephant's, 76, 274, 776, of hemi-
chordate, 17
- Trypsin, 321, 322, 323, 327
- Trypsinogen, 322
- Tuatara, 48
- Tube, digestive, 6, 12, 166, 263, 268, 522;
endocardial, 352, 353; Eustachian, 303,
397, 791, 792, 794; Fallopian, 437, 471,
479, 483, 487; medullary—see tube,
neural; neural, 163, 172, 349, 322, 674,
675; tracheal, 385
- Tuber cinereum, 711, 713
- Tubercle, genital, 489, 490; of rib, 522, 545,
546
- Tuberculosis, 187
- Tuberculum impar, 285, 286
- Tubule, collecting, 433, 434, 435; connect-
ing, 433, 435; convoluted, 433, 434, 435;
epididymal, 469; mesonephric, 486;
pronephric, 441; seminiferous, 457, 458
- Tubuli, contorti, 457, 458, 469; recti, 457,
458, 469
- Tubulidentata, 62, 71, 72
- Tumor, 185
- Tumuli, 114
- Tunic, 19, 208
- Tunica, adventitia, 344, 345; albuginea,
457, 463; fibrosa, of eye, 807, 809;
fibrosa, of kidney, 431; intima, 344;
media, 344; vaginalis, 457, 459; vasculosa,
of eye, 808, 809; vasculosa, of testis, 457
- Tunicates, 18, 19, 208, 273, 499; compound,
19
- Tunicin, 208
- Tupaia, 62
- Turacus, 249
- Turbinal, 403, 569, 570
- TURGENIEFF, 702
- Turkey, 57, 219, 243, 313
- Turtle, 43, 48, 49, 548; beak, 242; bladder,
269, 438; circulatory system, 334, 374;
digestive system, 269, 276, 282, 300, 305,
312; flipper, 631; reproductive system,
451, 452, 456, 461, 463, 475, 476, 480;
respiratory system, 386, 403, 408, 414;
shell, 196; skull, 567, 579; vertebral
column, 525, 533, 536, 539

- Turtle-dove, 420
 Tusk, 297, 299
 TWAIN, MARK, 188, 260
 Tympanic, 568, 573, 578, 579, 581, 596;
 cavity, 792, 793, 794, 798
 Tympanohyal, 568, 577
 Tympanum, 791
 Tyndall, blue, 248
 Type study, 3
 Typhlosole, 267, 268, 312
 Typhoid, 187, 332

 Udder, 223
 Uebergangsteil, 505
 Ulna, 607, 627, 628, 631, 632
 Ulnare, 627, 628
 Ultimobranchial, 500, 502, 503, 504
 Umbraculum, 829
 Unciform, 629
 Unequal growth, 162
 Unguis, 237, 238
 Ungula, 72
 Ungulates, 72-76, 92, 288, 294, 477, 530,
 730
 Unguligrade, 603, 637
 Urachus, 438
 Uræter, 431, 434, 436, 437, 439, 446, 457,
 461, 468, 469, 476, 478, 479, 481, 490
 Urethra, 434, 437, 438, 457, 469, 476, 477,
 479, 480, 481, 489, 490
 Urinary, bladder, 269, 270, 434, 437-439,
 457, 468, 476, 479, 481, 490; units, 432,
 433; vesicle, 446
 Urine, 428, 434, 435, 436, 506
 Urochordata, 17, 18-21
 Urodelæ, 39, 40, 41, 42
 Urodele, caudal ribs, 345; circulatory sys-
 tem, 365, 366, 367, 379; digestive sys-
 tem, 281, 293, 307; gonad, 456; larval
 skull, 559; trachea, 403
 Urogenital, canal, 437; opening, 489;
 sinus, 466, 476, 478, 479
 Urostyle, 532
 Uterus, 64, 65
 Uterine cervix, 479, 481, 483
 Uterovaginal canal, 488
 Uterus, 437, 468, 471, 474, 479, 483, 487,
 490, 495; bicornis, 484; bipartitus, 484;
 duplex, 484; simplex, 484
 Utriculus, 734, 786, 791, 792, 795, 796, 798
 Uvula, 277

 Vaccine, 191
 Vacuole, contractile, 428
 Vagina, 437, 468, 471, 473, 477, 478, 480,
 481, 483, 487, 490; double, 479; mascu-
 lina, 457, 468, 487, 488
 Vaginal blind sac, 479

 Valve, anal, 325; auriculo-ventricular, 360;
 bicuspid, 360, 361; branchiostegal, 415;
 Heisterian, 316; labial, 415; mandibular,
 415; maxillary, 415; mitral, 360; nostril,
 416; pyloric, 308; respiratory, 415; semi-
 lunar, 355, 356, 360, 361; sinu-auricular,
 361; spiral, 268; tricuspid, 360, 361; of
 veins, 345
 Vampire bat, 307, 309
 Vane, 243
 Varanus, 50, 579
 Vas, deferens—see ductus deferens; effere-
 ns—see ductulus efferens
 Vasa vasorum, 377
 Vegetal pole, 158, 168, 169
 Vein, 341, 344, 345, 368-377; adrenolum-
 bar, 376; allantoic, 349, 351; anterior
 cardinal, 369, 370, 371, 372; arygos, 375,
 376, 377; of birds, 375; brachiocephalic,
 376, 377; cardiac, 373; cardinal, 342,
 343; caudal, 351, 369, 371, 373, 375, 376,
 522, 527; coccygeo-mesenteric, 375; com-
 mon cardinal, 351, 354, 355, 369, 370,
 371, 372; coronary, 376; cutaneous, 373,
 374; development of, 370, 371; of elasmob-
 ranchia, 371; epigastric, 375; femoral,
 373, 374, 375; of frog, 373; hemiasyggos,
 375, 376; hepatic, 317, 342, 343, 354, 355,
 369, 370, 371, 372, 373, 375, 376; hepatic
 portal, 317, 342, 343, 369, 371, 373, 375,
 376; iliac, 371, 372, 373, 374, 375, 376;
 iliolumbar, 376; intercostal, 374, 375; in-
 terlobar, 435; jugular, 351, 372, 373, 374,
 375, 376, 541; mammary, 376; ompha-
 lomesenteric, 351; orbital, 374; pectoral,
 375; pelvic, 373; postcardinal, 267, 351,
 369, 370, 371, 372, 373, 376; postcaval,
 355, 361, 373, 374, 375, 376, 471; precaval,
 361, 373, 374, 375, 376; pulmonary, 343,
 355, 357, 361, 373, 406; renal, 375, 376,
 431, 434; renal portal, 343, 371, 372, 373,
 374, 375; of reptiles, 375; sciatic, 373,
 374; subcardinal, 371, 372; subclavian,
 370, 371, 372, 373, 375, 376; subintestinal,
 267, 351, 369, 370, 371; umbilical, 349;
 of urodeles, 373; valves in, 345; ventral
 abdominal, 371, 372, 373, 375; vertebral,
 374, 375; vitelline, 173, 348, 349, 350,
 351, 364, 370, 371
 Velum, interpositum, 704, 707, 708, 711,
 724, 725; medullary, 705, 710; respiratory,
 417; transversum, 507, 704, 723, 725
 Velvet, antlers in, 235
 Vena cava 343, 361, 373, 471
 Ventral, 7, 8
 Ventricle, of brain, 674, 705, 706, 707;
 fifth, 714; fourth, 705, 706, 707, 710,
 726; of heart, 354, 355, 356, 357, 363;

- lateral, 705, 706, 711, 712, 727, 729; left, 358, 359, 361; optic, 723; right, 358, 359, 361; third, 705, 706, 707, 711, 728
- Ventriculus laryngis, 425
- Venule, 341
- Vermiform appendix, 269, 313
- Vermis of cerebellum, 708, 709, 730
- Vertebra, 178, 522-539; amphicoelous, 530, 531; ball-and-socket, 525; caudal, 528, 531, 532, 533, 534, 536, 537, 539; cervical, 530, 531, 532, 533, 534, 535, 536, 537; differentiation of, 536; development of, 526; epiphyses, 529; heterocoelous, 530; intersegmental position, 526; lumbar, 531, 533, 536, 537; opisthocelous, 530; procoelous, 530; prominens, 535, 537; sacral, 531, 532, 533, 536, 537; saddle-joint, 530; thoracic, 523, 531, 533, 536, 537, 539; trunk, 532, 536
- Vertebral part of rib, 547
- Vertebrata (Vertebrates), 9, 17, 25-80
- Vesica, bicornis, 437, 438; duplex, 437, 438; simplex, 437, 438
- Vesicle, optic, 808; otic, 789; of Savi, 769, 771; seminal, 457, 469, 474, 481; urinary, 446
- Vestibule, of genitalia, 479, 480; of lungs, 409; of mouth, 275; of nose, 775
- Vibrissae, 250, 760
- Villi, 268, 314
- da Vinci, 646
- Vipera, 300
- Vireo, 57, 828
- Visceral brain, 703
- Vision, binocular, 828, 830
- Visual, axis, 807; center, 716, 717; purple, 813; violet, 813
- Vitamins, 309, 814
- Vitelline, circulation, 349, 350; membrane, 159, 452
- Vitreous, 807, 816
- Viverra, 64, 618
- Viviparous, 472
- Vivisection, 189
- Vocal, cords, 303, 422, 424, 425; sac, 422
- Voice, apparatus, 420-426; box, 304, 424, 425
- Vomer, 555, 568, 577, 580, 582, 587
- Vorare, 62
- Vortices, hair, 251, 252
- Vulture, 56
- WALCOTT, 98
- WALDEYER, 204
- Wallaby, 61
- WALLACE, 92, 93
- WALLER, 689
- WALLS, 815
- Walrus, 65, 66, 287, 299, 430, 470, 492
- WALTER, 106
- Warm-bloodedness, 331
- Wart hog, 73, 299
- Water, 262, 327; cell, 309; moccasin, 51
- Weapons, 114
- Weasel, 65, 253, 318
- WEATHERFORD, 206, 449, 457, 676, 795
- WEIDENREICH, 122
- WEISMANN, 454
- Whale, 58, 78-80; brain size, 702; integument, 198, 199, 222, 224, 242, 249, 254; respiratory system, 404, 405, 420, 426; skeleton, 518, 534, 547, 631; toothed—see odontoceti
- Whalebone, 242
- Wharton's duct, 276, 278, 279
- Wheel organ, 22
- Whip-poor-will, 57, 246
- Whirlpool, divergent, 252; of life, 261
- White matter, 686, 695
- Whitefish, 290
- Whiting, 307
- WHITMAN, 702
- Whorl, 259
- WIEDERSHEIM, 300, 500, 666
- WILDE, 115
- WILDER, 118, 350, 552, 651
- Windpipe—see trachea
- Wing, of bat, 630; of bird, 548, 630; of pterodactyl, 630; of sphenoid, 570, 591
- Wishbone, 622
- Wolf, 64, 65, 420; Tasmanian, 61
- Wombat, 61, 477
- Woodchuck, 66; marsupial, 61
- Woodpecker, 57, 96, 238, 283, 284
- WOODRUFF, 223, 431, 471, 671
- Wool, 252, 253
- Worm, 266
- Wren, 57
- WRIGHT, 339
- Wrinkles, 201
- Wrist, 628, 632, 636; bones, 627, 628, 631, 632, 633, 636
- X-chromosome, 138, 139, 458
- Xenopus, 43, 237, 282, 386, 397, 610, 612
- Xiphisternum, 549, 550
- Xiphoid, 552, 553
- X-rays, 310, 508
- Y-chromosome, 138, 139
- Yolk, 158, 168, 169, 173, 451, 451, 453, 454; plug, 170, 171; sac, 44, 166, 172, 173, 174, 486; stalk, 166, 173, 318
- Ypsiloid, 610, 611, 612

- Zebra, 73
Zeuglodon, 295
Ziphius, 425
Zona, granulosa, 508; pellucida, 159
Zone, degressive, 272; egressive, 272; in-
gressive, 272; progressive, 272
Zoön, 449
Zyg-, 523
Zygapophyses, 523, 532
Zygomatic, arch, 595; bone, 595
Zygote, 156, 448



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